Group Decision-Making in Meerkats (*Suricata suricatta*)

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Summary

Groups of social animals are common in nature and often remain cohesive despite variation in each member's needs and optimal activity. How and why individuals coordinate themselves within groups has long been a puzzle for behavioural ecologists. Recently, theories on group decision-making have greatly advanced but there is still a lack of empirical evidence about the applicability and the generality of such theories in animals. Within my PhD project, I addressed questions on group decision making in wild groups of meerkats (*Suricata suricatta*), cooperatively breeding mongooses with high reproductive skew, foraging as cohesive units. I tried to fill the gap between theory and empirical evidence by quantifying naturally occurring transitions of activities and conducting experiments.

Groups mainly risk losing their cohesiveness when individuals change activity. Such activity transitions are initiated by some group members, but complete transitions are only fulfilled when all members follow the initiator in its change of activity. Only then the initiator can be regarded as a leader. Changes of group activity result from various group decision-making mechanisms, yet, the differences between them are still not clear. In meerkats, I investigated initiation of activity change in two contexts (the emergence order from the burrow and the leaving order from the burrow area) and how this could be linked to leadership. I addressed how meerkat groups were renovating their sleeping burrow. I investigated who was involved in deciding when to move from one foraging patch to another and the underlying decision mechanism. Furthermore, I analysed several factors influencing spatial positioning within groups and the likely advantages and drawbacks of them. Finally, I elicited conflicts of interest between two individuals within a group to assess how individuals with divergent incentives are still able to remain in a cohesive group.

The initiation of activity changes in meerkats in two temporarily close contexts depended on different factors: individual identity was important for the emergence order, while foraging success explained the leaving order. Burrow renovation, a cooperative behaviour in meerkats, resulted from social facilitation. However, meerkats also used consensus decisions, particularly when they moved from one foraging patch to another. I demonstrated that a quorum of two to three individuals emitting moving calls was necessary before the group increased speed and changed to a new foraging location. Analysing the geometry of the group revealed that meerkats associated with some group members more often than with others, indicating some social preferences. In conflict situations, the first individual to move was usually followed, even by the individual who had a divergent incentive, emphasizing the importance of group cohesion for meerkats.

My thesis shows that within the same species a wide range of group decision-making mechanisms is used. Some activity changes are initiated by specific obvious signals and decisions are found by a quorum of the group. In other situations, the first individual to show an activity change is followed without any obvious decision periods to find a consensus between individual preferences. These observations indicate that not only initiators of an activity change, but also the followers with their decision to join or not, play an important role in the outcome of group decisions. Individuals appear highly responsive to each other at any time, which is likely to be crucial for animals living in an environment where group cohesion has high fitness benefits.

Zusammenfassung

In der Natur findet man häufig soziale Tiere in Gruppen, deren einzelnen Mitglieder in der Regel nahe zusammen bleiben, obwohl sie unterschiedliche Bedürfnisse oder optimale Aktivitätsmuster haben. Wie und warum Individuen sich in einer Gruppe aufeinander abstimmen ist für viele Verhaltensökologen noch immer ein Rätsel. In letzter Zeit wurden im Bereich der Gruppenentscheidungen grosse Fortschritte erzielt, es besteht aber immer noch ein Mangel an empirischen Beweisen über die Eignung und die allgemeine Gültigkeit solcher Theorien in Tieren. In meiner Doktorarbeit habe ich mich mit Fragen bezüglich Gruppenentscheidungen bei wildlebenden Erdmännchen (*Suricata suricatta*) befasst. Diese Mangustenart lebt in stabilen, sozialen Gruppen mit kooperativer Jungenaufzucht, wo die Fortpflanzung vorallem dem dominanten Paar zusteht, und sie gemeinsam auf Futtersuche unterwegs sind. Ich versuchte die Lücke zwischen Theorie und empirischen Beweisen zu füllen, indem ich natürlich vorkommende Aktivitätsänderungen quantifizierte und Experimente durchführte.

Gruppen riskieren ihren Zusammenhalt vor allem dann zu verlieren, wenn ihre Mitglieder die Aktivität ändern. Solche Wechsel werden durch einzelne Individuen initiiert. Allerdings ist ein vollständiger Aktivitätswechsel nur dann vollzogen, wenn letztendlich alle Mitglieder ihre Aktivität so ändern wie der Initiator. Erst dann kann der Initiator als Anführer betrachtet werden. Änderungen der Gruppenaktivität sind auf verschiedene Entscheidungsprozesse in der Gruppe zurückzuführen, deren Unterscheidung noch nicht ganz eindeutig ist. Ich untersuchte die Initiierung von Aktivitätswechseln bei Erdmännchen in zwei Situationen (die Reihenfolge des Auftauchens aus dem Bau und die Reihenfolge in der sie den Bau verlassen) und verdeutlichte, wie diese Verhaltensweisen in Zusammenhang mit Führerschaft gebracht werden können. Ich richtete, wie Erdmännchen Gruppen ihre Schlafhöhle renovierten. Ich untersuchte, welche Individuen an der Entscheidung beteiligt waren, wenn sie sich von einem Ort der Nahrungssuche zu einem anderen bewegten und welches der zu Grunde liegende Entscheidungsmechanismus war. Zusätzlich analysierte ich verschiedene Faktoren, welche die räumliche Verteilung in einer Gruppe beeinflussen, sowie deren Vor- und Nachteile. Schliesslich induzierte ich zwischen zwei Individuen in derselben Gruppe Interessenskonflikte, um beurteilen zu können, wie Individuen mit unterschiedlichen Motivationen im Stande sind in zusammenhängenden Gruppen zu leben.

Die Initiierung von Aktivitätsänderungen bei Erdmännchen in zwei zeitlich nah aufeinanderfolgenden Situationen ist von verschiedenen Faktoren abhängig: Die individuelle Identität war wichtig für die Reihenfolge des Auftauchens aus dem Bau, während Erfolg bei der Nahrungssuche die Reihenfolge des Verlassens erklärte. Die Renovation des Baus, ein kooperatives Verhalten bei Erdmännchen, basiert auf einer soziale Aufforderung. Dennoch machten die Erdmännchen auch Konsensentscheidungen, insbesondere dann, wenn sie sich von einem Futterplatz zu einem anderen bewegten. Ich demonstrierte, dass eine Mindestanzahl von zwei bis drei Individuen nötig ist, die alle spezifische Rufe ausstossen, bevor die Gruppe ihr Tempo erhöht und ihren Futterplatz ändert. Die Analyse der Gruppengeometrie ergab, dass Erdmännchen soziale Präferenzen zeigten, da sie bevorzugt mit einzelnen Individuen interagierten. In Konfliktsituationen wurde dem ersten sich bewegenden Individuum gefolgt, einschliesslich desjenigen Individuums, das durch meine Manipulation eine andere Motivation hatte. Dies zeigt, wie wichtig der Gruppenzusammenhalt für Erdmännchen ist.

Meine Doktorarbeit verdeutlicht, dass innerhalb der gleichen Art mehrere unterschiedliche Mechanismen in Gruppenentscheidungen benutzt werden. Einige Aktivitätswechsel werden durch klare, spezifische Signale initiiert und Entscheidungen werden von einem Quorum der Gruppe getroffen. In anderen Situationen wird demjenigen Individuum gefolgt, das eine Aktivitätsänderung zeigt, ohne dass vorher ein ersichtlicher Konsens über die individuellen Präferenzen getroffen wurde. Diese Beobachtungen zeigen, dass sowohl die Initiatoren einer Aktivitätsänderung, wie auch die Individuen, welche die Entscheidung treffen den Initiatoren zu folgen, für den Ausgang von Gruppenentscheidungen eine wichtige Rolle spielen. Die Individuen scheinen sehr stark aufeinander zu reagieren; dies könnte insbesondere für gruppenlebende Tiere ausschlaggebend sein, welche in einer Umwelt leben, wo der Gruppenzusammenhalt grosse Fitnessvorteile mit sich bringt.

Résumé

Les groupes d'animaux sociaux sont fréquents dans la nature et restent souvent cohésifs malgré des différences entre les besoins et les activités optimales de chaque membre. Comprendre comment et pourquoi des individus parviennent à se coordonner entre eux représente depuis longtemps un challenge pour de nombreux écologistes comportementaux. Récemment, les théories sur la prise de décision collective se sont beaucoup développées, mais il y a encore un manque de preuves empiriques quant à l'applicabilité et la généralité de telles théories chez les animaux. Durant ma thèse de doctorat, je me suis intéressé à la prise de décision collective dans des groupes de suricates (*Suricata suricatta*) vivant à l'état sauvage. Cette mangouste se reproduit coopérativement, présente un fort biais de reproduction et recherche de la nourriture en unités cohésives. J'ai essayé de combler l'écart entre théories et preuves empiriques, en observant des transitions d'activités naturelles et en conduisant des expériences.

Un groupe risque surtout de perdre sa cohésion quand les individus qui le composent changent d'activité. De telles transitions d'activité sont initiées par certains membres. Toutefois, les transitions complètes d'activité ne sont finalisées que quand tous les membres du groupe ont suivi l'initiateur dans son changement d'activité. Ce n'est qu'alors que l'initiateur peut être considéré comme un leader. Les changements d'activité de groupe résultent de divers mécanismes de prise de décision collective. Toutefois, leurs différences sont encore mal comprises. Chez les suricates, j'ai déterminé l'initiation d'un changement d'activité dans deux contextes (l'ordre d'émergence du terrier et l'ordre de départ de la zone du terrier) et dans quelles mesures cela pouvait être lié au leadership. J'ai aussi analysé la rénovation des terriers dans lesquels les suricates passent la nuit. J'ai également identifié quels individus prenaient la décision de quitter un site de recherche de nourriture pour un autre ainsi que les mécanismes de décision mis en jeu. De plus, j'ai analysé les différents facteurs influençant le positionnement spatial d'un individu au sein d'un groupe ainsi que les avantages et inconvénients qui peuvent en découler. Enfin, j'ai induit des conflits d'intérêts entre deux individus d'un même groupe afin de déterminer comment des individus dont les motivations divergent sont néanmoins capables de demeurer dans un groupe cohésif.

Chez les suricates, l'initiation d'un changement d'activité dépend de différents facteurs dans deux contextes proches temporellement : l'identité de l'individu est importante pour l'ordre d'émergence du terrier, tandis que le succès lors de la recherche de nourriture explique l'ordre de départ. La rénovation du terrier, un comportement coopératif pour les suricates, résulte d'une facilitation sociale. Toutefois, les suricates ont également recours à des décisions consensuelles, notamment lorsqu'ils se déplacent d'un site de recherche de nourriture à un autre. J'ai mis en évidence qu'un quorum de deux à trois individus émettant des cris de déplacement est nécessaire avant que le groupe n'accélère et ne change de zone de recherche de nourriture. L'analyse de la géométrie du groupe a révélé que les suricates s'associent plus souvent avec certains membres du groupe qu'avec d'autres, démontrant l'existence de préférences sociales. Lors de situations conflictuelles, le premier individu initiant un mouvement est généralement suivi, même par un individu ayant une motivation divergente, soulignant l'importance de la cohésion du groupe pour les suricates.

Ma thèse de doctorat montre qu'un large spectre de mécanismes de prise de décision collective peut être employé au sein d'une même espèce. Certaines

transitions d'activité sont initiées par des signaux spécifiques évidents et les décisions sont prises par un quorum dans le groupe. Dans d'autres situations, le premier individu à changer d'activité est tout simplement imité par les autres membres du groupe sans la moindre période de décision permettant d'établir un consensus entre les préférences des individus. Ces observations démontrent non seulement l'importance qu'ont les initiateurs d'un changement d'activité dans l'issue des décisions de groupe, mais aussi celle des suiveurs avec leur décision de se joindre ou non. À tout moment les individus apparaissent très réceptifs aux autres, caractéristique cruciale pour des animaux vivant dans un environnement où la cohésion du groupe confère d'importants avantages en termes de succès reproducteur.

GENERAL INTRODUCTION

General Introduction

1. BACKGROUND ON GROUP DECISION-MAKING

In its broadest definition, sociality starts when two individuals or more spend time together. Thereby, such social units can organize themselves along a wide range of modes of group-living (Lee, 1994), depending on the life-history traits of the species they belong to (Krause & Ruxton, 2002). Some animal aggregations are due to the mere attraction of each individual towards an external cue such as light (Parrish & Edelstein-Keshet, 1999). In these aggregations, even in the absence of specific social interactions (Hinde, 1976), specific patterns and properties can arise at the group level (Parrish & Edelstein-Keshet, 1999). Animal groups are also commonly found in the absence of any attracting external cue. Then, social interactions gain substantial importance and group members weigh up the costs and benefits of grouping to assess whether or not to stay in the group (Krause & Ruxton, 2002). Many factors impact on this ratio between costs and benefits of grouping. The most influential of these factors is group size (Krause & Ruxton, 2002). For instance, gathering together can help group members to detect predators (Powell, 1974). However, if too many group members join, costs like increased likelihood of ectoparasite transmission are likely to appear (Hoogland & Sherman, 1976; Hoogland, 1979). As a result, observed group sizes are often a compromise between insiders' (i.e., actual group members which could face higher costs if another individual joins the group) and outsiders' (i.e., potential group member which could enhance its benefits by joining a group) estimations of grouping advantages (Higashi & Yamamura, 1993; Dittmann et al., 2005). Another important feature of a group is its social composition. For example, when dispersing individuals try to establish themselves in another group, they should take into consideration the sex-ratio of potential groups and choose for the group with the least number of individuals of its own sex (Lee, 1994). Finally, the stability and the persistence of the group through time also influence grouping advantages. All of these factors lead to an important but limited number of potential social organisations. Thus, Lee (1994) describes 7 levels of sociality and 18 levels of core social states. All of the non-solitary forms of living need some sort of coordination between grouping individuals. Yet, evolutionary pressures to select for efficient coordination mechanisms are highest in persistent

groups. Studies on group decision-making therefore focus on such groups. Depending on whether or not group membership is identical through time, one can distinguish two types of persistent groups. In fission-fusion groups, individuals or sub-groups can join or leave the main group (Kummer, 1968; McFarland Symington, 1990). On the other hand, in stable groups, group membership can last for a long period of an individual's lifetime (Rasa, 1987).

(a) ***Typology of group decisions***

Group decisions refer to any decisions taken by social animals when belonging to the same group. Two types of group-decision mechanisms have been described so far. In consensus decisions, "members of a group choose between two or more mutually exclusive actions with the specific aim of reaching a consensus" (Conradt & Roper, 2005). If only one individual controls the group choice (and the others abide by this choice), the group has done an "unshared consensus decision". Unshared consensus decisions can for example happen when an individual is stronger than its other group mates and can monopolize foraging resources (King et al., 2008) or when an individual in the group has more information about the group's environment than the others (Lusseau & Conradt, 2009). As soon as two or more group members intervene actively in the consensus building, it becomes a "shared consensus decision" (Conradt & Roper, 2005). In contrast, in combined decisions, "members of a group choose individually (but not necessarily independently) between two or more actions. They do not aim for consensus but the combined results of their decisions usually affect the group as a whole" (Conradt & Roper, 2005). This combination of individual strategies lead to an adaptive equilibrium between activities at the group level (Conradt & List, 2009).

Both decision types enable to integrate individual behaviours of group members in a group behaviour via aggregation rules, even if such rules have not been described for combined decisions so far (Conradt & List, 2009). In consensus decisions, most of these rules include an information-pooling phase during which individuals can exchange their knowledge about the decision to be taken (Conradt & Roper, 2005). During this phase, individuals can express their preference reflecting voting behaviour and the group will abide by the choice of a specific threshold (List, 2004). Such thresholds are usually called "quorums", which are defined as the "minimum number of group members that need to take or favour a particular action

for the whole group to adopt this action" (Conradt & Roper, 2005). Their use is widespread in animal groups (Prins, 1996; Franks et al., 2003; Seeley & Visscher, 2003; Pratt et al., 2005; Ward et al., 2008; Petit et al., 2009; Sumpter & Pratt, 2009; Sueur et al., 2010). As an example, before moving in a specific direction, female African buffalos in a herd will point their head in the direction of their choice and the group will move cohesively in the direction in which most individuals pointed (Prins, 1996).

At the end of the group decision-making process, animal groups either remain united or split into sub-groups. Theoretically, both types of group-decision (consensus and combined) can lead to both types of group-decision outcomes (united or split). The most common relationships are that a consensus decision will keep the group united and that a combined decision will lead to more frequent group splits (Conradt & Roper, 2005; Kerth, 2010). However, consensus decisions within a group can sometimes lead to the separation of the group, as is the case in humans when a couple divorce by mutual consent (Peters, 1986). This link between consensus and group split is far more difficult to show in animals as it is currently nearly impossible to differentiate between animal group splits due to different individual choices or due to overall agreement. Furthermore, combined decisions do not have to lead to group split, particularly when a group faces a choice of activities while remaining stationary.

(b) ***Spatial positioning within animal groups***

The fact that some positions within a group could be more beneficial than others have been considered for a long time (Hamilton, 1971). However, until recently, recording the positions of group members required a considerable effort and was not accurate enough to fully describe a group behaviour. For instance, recordings of nearest neighbour distance was often done on few individuals at the same time and were classified as categories (Robinson, 1981; Boinski et al., 1994). Furthermore, the study of a group's spatial structure always necessitated the presence of human observers. Such constraints can be overcome by the use of portable GPS devices (Pochron, 2001; Winnie et al., 2006). The ability to equip several individuals at the same time, to have access to precise measurement of any distance between group members and to enable recordings even in the absence of human observers allowed the discovery of so far undefined phenomena. For instance, it has recently been shown in two different species (cows and pigeons) that social dominance correlates with

average position within the group (Nagy et al., 2010; Šárová et al., 2010). A permanent recording of spatial positions could also enhance our understanding of interactions between individuals. So far, most of the studies on social interactions (grooming, dominance…) did not control for inter-individual distances (Rowell, 1968; Seyfarth, 1976; Kutsukake & Clutton-Brock, 2006). This lack of control could have impeded to distinguish various individual strategies within the groups: some subordinate might submit a lot to dominants because they stay close-by while other subordinates are not seen submitting because they remain away from the dominants. This effect could in turn be integrated into social network analyses, which depend upon data as precise and large as possible (Whitehead, 2008). Social network analyses give in return important insights on a group's organisation, like preferred associations (Nituch et al., 2008; Wolf & Trillmich, 2008; Gygax et al., 2009; Ramos-Fernández et al., 2009).

(c) *Leadership*

A temporal approach of group decision-making brings many insights on the decision-making mechanisms used in animals (Sueur et al., 2010). With this approach, one can describe in which sequence group members join in a new activity. Traditionally, individuals starting an activity first have been seen as "leaders" (Reinhardt, 1983). Leadership can be constant through time, with the same individual leading repeatedly (Reinhardt, 1983; Dumont et al., 2005). In this case, leadership can be seen as a property of the leading individual. Sometimes, this property can be scaled along another individual characteristic. For instance, in cows, the ability to control the travel direction of the group is increasing with increasing dominance rank, which has been described as "graded leadership" (Šárová et al., 2010). A constant leadership can also result from the previous history of a group. It has been theoretically shown that in a group of two identical foragers, the first to drop below its energetic needs (by random fluctuations) will lead the pair to forage again. The worst forager of the pair will remain leader for an extended period of time (Rands et al., 2003). However, when individuals differ in their metabolic requirement or in their predation risk, the role of energetic needs on leadership becomes less clear (Rands et al., 2008). Finally, leadership can be distributed across all group members, with all individuals able to lead the group on different occasions (Leca et al., 2003; Šárová et al., 2007). This last

type of leadership can also be seen as a total absence of leadership as individuals lead "an equal proportion of the observed collective moves" (Gautrais, 2010).

Recent research focused on the fact that leaders are not always successful and that they sometimes stop and fail in their attempt to initiate a change in activity or direction (Petit et al., 2009; King, 2010). This finding reveals the need to clarify the terminology. Lately, King (2010) defined "initiators" as individuals within a group who start an activity first, and "leaders" as initiators followed by the rest of the group in their activity change (i.e., leaders are "successful" initiators). Therefore, if initiators are to become leaders, they can influence their fellow group members by increasing their initiation rate (Conradt et al., 2009; Gautrais, 2010), by directly emitting specific signals to attract followers (Radford, 2004) and/or by monitoring the reaction of followers to their lead (Sueur & Petit, 2010). It is also already known that social affinity (Bonanni et al., 2010) or personality (Harcourt et al., 2009; Michelena et al., 2010) render some individuals more likely to become followers. Yet, research on the behaviour of followers still need to be deepened as well as our understanding of why individuals follow (van Vugt, 2006; King et al., 2009).

(d) ***Individual variation***

Animal groups are never formed of individuals that have identical needs or preferences and this variation is likely to strongly influence leadership and group decision-making mechanisms. For instance, group members can vary in their assertiveness towards their optimal goal. It has been shown that some group members are more willing to give in than others (Lamprecht, 1996; Couzin et al., 2005; Freeman et al., 2011; Šárová et al., 2010). Lamprecht (1996) made an important insight when he claimed that leadership can result from individual differences between group members' "critical distance". The critical distance represents how far an individual can spatially separate before this individual needs to come closer to its partner(s). Logically, an individual with the highest critical distance will emerge as a leader because other group members will always join him before he joins them. This importance of assertiveness received recent empirical evidence. In cattle (Šárová et al., 2010) and common pigeons (Freeman et al., 2011), individuals with the highest assertiveness to their goals actually emerge as leaders. However, being too assertive for an individual can be detrimental to its success as a too high assertiveness increase the frequency of group splits (Couzin et al., 2005; Conradt et al., 2009).

Consistent individual variation across time and context in behavioural traits is a prerequisite of the framework of animal personality (Gosling, 2001; Réale et al., 2007; Bell et al., 2009). Animal personalities could provide new perspectives to the study of group decision-making (Kurvers et al., 2009; Michelena et al., 2010). Recently, leadership in barnacle geese has been shown to correlate with novel-object score (Kurvers et al., 2009), even if the effect tended to be diluted in large groups (Kurvers et al., 2011). Furthermore, groups with different proportions of several personality types behave differently and, usually, groups of mixed composition perform better (Pruitt & Riechert, 2011) or are more flexible (Michelena et al., 2010). Indeed, groups of "docile" and "aggressive" spiders have a higher foraging efficiency than groups with only one personality type (Pruitt & Riechert, 2011) and groups of "shy" and "bold" sheep foster more frequent social coordination than uniform groups, leading to an increased behavioural plasticity for mixed groups (Michelena et al., 2010).

2. AIMS OF RESEARCH

There is a wide range of described group decision-making mechanisms and I aimed to assess how diverse were meerkats in using these various mechanisms. In general, to study group decision-making in animals, it is crucial to possess extensive knowledge of the composition of the group and of the individual characteristics of each group member. Furthermore, studies with groups in their natural environment are important to assess the outcome of all external factors (such as weather, predation, competition…) on group decision. My thesis conducted with habituated animals in their natural habitat includes both criteria. Meerkats have a highly skewed reproduction in favour of dominant individuals and are strictly social. They also belong to a clade of related species with different social organization. For instance, banded mongooses have little reproductive skew (Furrer, 2009). This setting offers a unique opportunity to assess whether individuals monopolizing reproduction also monopolizes group decisions or whether dominants need to share decision-making to ensure the presence of subordinates in the group.

3. STUDY SPECIES

Phylogenetically, meerkats are mammals belonging to the Order Carnivora and to the Family Herpestidae (Agnarsson et al., 2010). They are social mongooses living in groups and form a common clade with all the other group-living mongoose species (Veron et al., 2004). Meerkats are highly specialised for arid environments and possess an unusually low basal metabolic rate for Carnivora enabling them to forage for longer periods at higher ambient temperatures (van Staaden, 1994). Meerkats are widely distributed in the southern part of Africa, mainly in arid areas (van Staaden, 1994), are easily habituated to human presence (van Staaden, 1994) and are not currently threatened (Macdonald & Hoffmann, 2008). Each meerkat group needs a relatively large territory defended against neighbouring groups (van Staaden, 1994) and consisting of several underground sleeping burrows (Thornton et al., 2010).

Meerkats form stable associations for all their daily activities and can therefore be classified under the sixth level of sociality recognized by Lee (i.e., stable associations for all activities, 1994), a rare phenomenon in Carnivora (Holekamp et al., 2000). Furthermore, meerkat groups are composed of related females and males (apart from when a new dominant male immigrates in a group) and are therefore an example of the fifteenth core social state defined by Lee (i.e., kin males and females living together, 1994). Meerkat groups have sizes ranging from 2 to 50 individuals (Clutton-Brock et al., 1999a) and show a slightly biased sex-ratio in favour of males (van Staaden, 1994). In each group, one female and one male act as dominant individuals and all the remaining individuals are considered subordinates (Clutton-Brock et al., 1999b). The dominant pair monopolizes reproduction within the group and produce about 80 % of the pups (Griffin et al., 2003). To ensure their control on reproduction, dominant females actively evict rival subordinate females, who can either join the group once the dominant female's pups are born or try to establish a new group (Clutton-Brock et al., 1998). However, dispersal in meerkats is mainly done by roving males trying to gain dominance in another group (Doolan & Macdonald, 1996b).

In addition of being highly social, meerkats display many cooperative activities (Clutton-Brock et al., 2002). First, meerkats reinforce their social relationships within the group by grooming each other and stabilize dominance status (Kutsukake & Clutton-Brock, 2006). Second, when foraging in groups, satiated meerkats climb on trunks or shrubs to go on sentinel duty (Clutton-Brock et al.,

1999c). While on guard, sentinels emit regular sentinel calls, which allow other foraging individuals to invest more time in search of food (Manser, 1999). When sentinels spot a potential danger, they also warn other group members through a sophisticated system of alarm calls (Manser, 2001). Third, in their arid environment, meerkats often have to renovate their sandy burrow or boltholes (Clutton-Brock et al., 2002). This investment in social digging enables meerkats to always have safe locations to run to when a danger is discovered. Fourth, as meerkats pups are born with ears and eyes closed (van Staaden, 1994), they need constant protection while they are not able to leave the group's sleeping burrow with the rest of the group. This protection is mainly provided by adult non-breeders who remain at the burrow with the pups for an entire morning or day (Clutton-Brock et al., 2000). This protection is costly as babysitters suspend foraging activity during their duty. Finally, when the pups are able to follow the foraging group but are still not skilled enough to chase for their food, adults bring them food (Clutton-Brock et al., 2001; Thornton, 2008) and teach them prey-handling skills (Thornton & McAuliffe, 2006).

4. STUDY SITE AND POPULATION

The data presented in this dissertation were collected from August 2006 to November 2008 on the wild but habituated population of meerkats at the Kalahari Meerkat Project, near Van Zylsrus in South Africa (26° 58' S, 21° 49' E). The study population consisted of about fourteen habituated groups on which detailed observations and experiments can be carried out. The number of available groups fluctuated slightly from year to year due to diseases, emigrations outside the study area and fission of groups over 50 individuals in separate groups. Habituation of newly found groups take up to one year before researchers can collect data. Group sizes in the study population ranged from 6 up to 50 individuals. However, I conducted all my observations and experiments in groups of less than 20 individuals to ensure that I could observe all individuals at the same time. This group size category was the most common one at the study site during my observation period. The Kalahari Meerkat Project is running since 1993 and numerous workers have compiled an impressive dataset over the years. I took advantage of the long-term dataset in several parts of my study. Each group is routinely visited up to 4 times a week for 3-hours sessions in the morning and for 1.5-hours sessions in the evening.

Groups are located by radio tracking radiocollars fitted around the neck of at least one group member (Jordan et al., 2007). This technique does not entail any cost for the equipped individual (Golabek et al., 2008).

The study area is arid, with less than 250 mm of annual rainfall on average. The wet season can last from October to April with much of the rain falling in a limited number of heavy storms (Clutton-Brock et al., 1999a). During the hot and wet summer (October to April), mean monthly temperature is above 20 °C with maximum temperatures sometimes exceeding 40 °C. During the dry and cold winter (May to September), mean monthly temperature is below 20 °C and overnight frosts are common (Doolan & Macdonald, 1996a). The vegetation is mainly concentrated on the dunes with annual and perennial grasses (lovegrass, threeawns, sourgrass, and *Schmidtia* spp.). Ligneous vegetation consists of dispersed shrubs (three-thorns) and trees (camel-thorns and shepherd's tree).

In this habitat, meerkats often interact with ground squirrels, yellow and slender mongooses and a variety of birds following the foraging pack (fork-tailed drongos, southern yellow-billed hornbills and crowned lapwing). At the study site, meerkats can also encounter non-threatening animals (such as cape hares, gemsbok, springbok, eland, blue wildebeest, hartebeest and ostrich). Their major predation threat comes from birds of prey (several eagle species and pale-chanting goshawk) and black-backed jackals. Occasionally, African wild cats and caracals can be seen. Snakes are common in the area (including the two poisonous snakes, Cape cobra and puff adder). Springhare, aardwolf, aardvark and porcupine are potential nocturnal sightings at the Project.

5. OUTLINE OF THESIS

The thesis covers a wide area of group decision-making research. With observations and experiments, I examine which are the mechanisms underlying various decisions meerkats face throughout their daily activities. In the **first chapter,** I investigate leadership in two temporally close activity transitions to assess whether leadership is constant across contexts. To do so, I compare the factors explaining leadership when meerkats emerge from their burrow with the ones explaining leadership when meerkats leave their burrow system to initiate foraging. In **chapter 2**, I focus on sleeping burrow renovation, a specific activity meerkats display while they

are still at their burrow. With detailed observations, I test whether the organisation of burrow renovation is due to social facilitation and/or to the use of specific signals. In **chapter 3**, I describe the effect of a vocalisation meerkats use before changing foraging patch, the "moving" call. In particular, I observe how many individuals are involved in a moving call chorus and how this affects the increase of group speed. This chapter therefore assesses whether a quorum of individual is needed for meerkat groups to change their foraging patch. In **chapter 4**, I describe the relative spatial positions of different group members and their impact on group structure. For this purpose, I used direct observations and recordings from precise GPS collars. In **chapter 5**, I analyse the resolution of conflicts of interest. To that end, I induce conflicts of interest within a group by rewarding two individuals in different locations. I then describe how the trained individuals are solving the conflict. In the **general discussion**, I discuss my results and their implications in the general framework of group decision-making in animals.

Overall, this study sheds light on many aspects of theoretical interest, and particularly on the importance of individual variation for group-living phenomena. Data in chapter 1 to 5 have been collected with the specific aim to test theoretical predictions. In particular, I wish to understand the link between activity initiation and leadership and the influence of conflicts of interest on group decision-making. Empirical data on these aspects still remain scarce on animal groups in the wild and my study is a step in the direction to bridge the gap between theory, observations and experiments.

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CHAPTER 1

Individual Variation in Initiating Two Temporally Close Group-activity Transitions in Meerkats (*Suricata suricatta*)

To be submitted

Individual Variation in Initiating Two Temporally Close Group-activity Transitions in Meerkats (*Suricata suricatta*)

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To be submitted

Summary

Models predict that an individual shifts activity when it is optimal according to its needs. However, in social groups, this activity shift can be influenced by other group members. Individuals shifting activity first are identified as initiators. When joined by other group members, successful initiators become leaders. By inciting others to join their optimal shifts, leaders are predicted to increase their grouping benefits. To determine the dynamic of group coordination, one should assess whether initiators are consistently the same over different contexts and over time, and their probability to become leaders. Here, we analysed two activity transitions in meerkats. First, we focused on the emergence from the burrow. For this transition, the probability to initiate was unequally shared: the same individuals were emerging first more often than expected. This was not explained by previous foraging success or individual characteristics. Second, we analysed the leaving order from the burrow to start foraging. In this context, the likelihood for individuals to initiate was more variable and correlated with physiological needs. Therefore, the two transitions differed in their organisation. Emergence order might reveal "personality" differences among individuals while leaving order might reveal the influence of inner state on the onset of cohesive foraging. Our study shows that different mechanisms can underlie leadership in temporally close yet varied contexts.

Keywords: activity transition; initiation; leadership; consistency; internal state; personality; meerkats

1. INTRODUCTION

Changing activity is relatively easy for an individual on its own: it just needs to assess when it is optimal for it to do something else, according to its internal state and to conditions given by the surrounding environment (Krebs & Davies, 1978). However, when living in groups, an individual about to change activity can be influenced by other individuals (Reinhardt, 1983). Within a group, initiating a new activity might be important for an individual to increase its grouping benefits, for instance by accessing food first (Reebs, 2000). This should be the case in most contexts, expect maybe in highly perilous activity changes (e.g., when zebra herds have to cross crocodile-infested rivers). When an initiator succeeds in attracting followers to its new activity, it is recognised as a "leader" (King, 2010).

When an initiator has been joined by the rest of the group (i.e., when an initiator became a leader), it is considered that the group took a consensus decision (Conradt & Roper, 2005). To reduce consensus costs, variable leadership (when many individuals in the group can act as leaders on different occasions, Conradt & Roper, 2005) is expected to be widespread in animals, unless leaders have much higher quality information than followers (Conradt & Roper, 2003). Many empirical studies in various taxa have tried to understand why and how some individuals become leaders (fish: Reebs, 2000; Harcourt et al., 2009; birds: Lamprecht, 1992; Biro et al., 2006; Kurvers et al., 2009; farm animals: Reinhardt, 1983; Dumont et al., 2005; Šárová et al., 2007; primates: Erhart & Overdorff, 1999; Barelli et al., 2008). Two of these studies found a variable tendency for individuals to become the leader of their group (Lamprecht, 1992; Šárová et al., 2007) and therefore matched the theoretical prediction. However, several recent studies found a constant leadership (*i.e.*, same individual leading repeatedly) in their study population, at least during specific periods of the year (Reinhardt, 1983; Erhart & Overdorff, 1999; Reebs, 2000; Dumont et al., 2005; Biro et al., 2006; Barelli et al., 2008; Harcourt et al., 2009). Furthermore, contrary to theoretical expectations, in four cases, researchers were not able to link the leader's consistency to a higher amount of information but to other features: its rank in the dominance hierarchy (Biro et al., 2006), its body size (Reebs, 2000) or its personality (Harcourt et al., 2009; Kurvers et al., 2009).

Whilst these studies are informative in understanding variability in animal leading behaviour, the majority have focused primarily on one context. Only two studies in farm animals elucidated the influence of context on leadership and found different organizations in different contexts (Reinhardt, 1983; Dumont et al., 2005). To better understand the dynamics of groups in general, it is crucial to investigate leadership in different natural contexts in wild animals. This will help to understand whether various types of leadership have to be expected in various contexts. In particular, if these contexts are temporally close to each other, it will allow us to make inferences on the causes found in the variation of leadership.

Meerkats are a good model to study such morning transitions. They live in the Southern Kalahari and form cohesive social groups. They sleep underground using burrow systems in open land, and each morning have to decide when to leave their burrow. In this first context, groups have to coordinate their exit from a safe location and expose themselves to a higher risk of predation. Once they emerge, they either renovate their burrow (Bousquet & Manser, in prep.), warm their body by standing on their hind legs with their torso facing the sun ("sunning" position), groom each other (Kutsukake & Clutton-Brock, 2006), or play (Sharpe, 2005). However, at some point, meerkats will start heading in a specific direction to start foraging. In this second context, groups have to coordinate the start of their foraging route. In both contexts, the shifts in activity rarely happen at the same time for each group member. Therefore, at least some group members (the initiators) need to wait for the others to reach them or some (the followers) need to accelerate to join the rest of the group. If the initiators are not joined, they usually turn back to their group or go roving on their own, i.e. leaving the group to explore mating or immigration opportunities in other groups (Young et al., 2007). If they are joined, according to King's (2010) definition, they can be regarded as leaders for that activity change.

The aim of this study was to investigate if specific intrinsic characteristics (*e.g.* social status or personality) of a focal meerkat could explain its leading behaviour before foraging or whether it was more the foraging success of a meerkat that could explain better the order of emergence and leaving. If the investigated intrinsic characteristics have an important influence, this should be reflected by a consistency of emergence order and/or leaving order over days. Conversely, a high influence of fluctuating foraging success should be reflected by a variable emergence order and/or leaving order. We furthermore investigated whether both orders were

correlated to assess the influence of context on leadership: a positive correlation would indicate that leadership is consistent across contexts, and suggest that similar mechanisms may underlie group decisions.

2. MATERIAL AND METHODS

(a) *Study site and population*

We studied morning activity transitions in meerkats on the wild but habituated population of the Kalahari Meerkat Project (KMP), on ranchland in the South African Kalahari, near Van Zylsrus (26° 58' S, 21° 49' E). Data were collected during more than 100 group-hours of observations, between August 2006 and November 2008. Description of habitat and climate are provided elsewhere (Clutton-Brock et al., 1999a; Russell et al., 2002). All animals in the population could be individually identified by the use of unique dye mark combinations. Individuals were habituated to close observation (< 1 m). The ages of almost all individuals were known precisely (± 5 days) as well as most of their life-history events (except on immigrants, < 5 % of the individuals). Weight data were collected as often as 3 times a day (morning, lunch and evening). In meerkats, dominant individuals are usually by far the oldest individuals of their group. Therefore, we restricted all our analysis of social status to groups in which at least one subordinate was older than the age of the youngest dominant individual minus 90 days (results are qualitatively similar with other thresholds and also when all adults are included).

For this study, we collected data on emergence and leaving orders for 11 habituated groups (group size varying from 3 to 20 individuals) from September 2006 to March 2007 and from July 2007 to October 2007, including over 130 individuals. Due to birth, death, evictions and roving events, group sizes of each focal group changed during the observation period, but within a small range. For the assessment of the influence of foraging success and baby-sitting activity on emergence and for the repeatability of being the first up, we used the long-term database of the KMP. We extracted weight data, identity of baby-sitters and identity of the first individual up from 13 different groups between 1999 and 2008. This allowed us to additionally assess the effects that the smaller sample size of our data could not include (*e.g.* sex effects, reproductive stage effects). We used the presence of pregnant and lactating females in a group as an estimate of the breeding season for that group. When pregnant females were in the group, we considered the group as being in a

"Pregnancy" period. As soon as lactating females were in the group, the group was considered in a "Lactation" period.

(b) ***Emergence order***

We analyzed the emergence order from more than 100 mornings in 11 groups. For each individual, we computed a relative order score (RO) by using the following formula (Barelli et al., 2008):

$$RO = (R_i - 1) / (N - 1) \qquad (1)$$

where R_i is the emergence rank of the individual *i* and N is the total group size. Therefore, RO varies from 0 if the individual was the first one to 1 if the individual was the last one. During the breeding season, some subordinate females can be subject to overt aggression (Young et al., 2006) and some males can go roving (Young et al., 2007). Sometimes, these individuals emerge much earlier than the rest of the group and immediately leave the burrow area and remain the rest of the day on their own. As we were interested in the behaviour of the majority of the group, we discarded these individuals for that morning.

(c) ***Leaving order***

We recorded each movement of any meerkat travelling further than 10 m away from the mainly used entrance of their sleeping burrow as well as its direction. We retained this threshold to maintain consistency with a previous study on the same population (Turbé, 2006) and also because meerkats rarely go further without being followed. However we discarded all movements that did not attract all other group members: we focused our attention to the initiation made by the last individual before all other group members joined. Therefore, this individual was the leader in the sense of King (2010). Once a meerkat had been able to attract the rest of the group, we considered the leaving process over. The use of the equation (1) allowed us to determine a relative order in the leaving process for each individual. Then, this order score was compared to the emergence order score to assess whether both scores were correlated, within each morning. If potential evictees or rovers were still around (i.e. when they emerged with the rest of the group), we kept them in the analysis as they were able to attract the rest of the group in the same way as any other individual.

(d) ***Similarity of contexts***

We considered the emergence order and the leaving order as being two types of transition involving leadership for three reasons. First, meerkats emerge from usually one entrance of their burrow or to spatially close ones. Yet, if one digs out a meerkat burrow, one realises that burrow chambers are linked to many different entrances far apart. Therefore, even if we could not see what happened below ground, we can assume that meerkats follow each other below ground. Second, the temporal aspects of the activity transition are similar in both contexts (only on a different scale): the latency between the second and the first individual is on average twice as much as the latency between the third and the second individual and this difference is highly significant (emergence order: $latency_{2\rightarrow1}$: 322 ± 53 s, $latency_{3\rightarrow2}$: 159 ± 23 s, generalised mixed-effect model, $\chi^2 = 4936$, $df = 1$, $p < 0.001$; leaving order: $latency_{2\rightarrow1}$: 55 ± 13 s, $latency_{3\rightarrow2}$: 29 ± 7 s, generalised mixed-effect model, $\chi^2 = 743$, $df = 1$, $p < 0.001$). Third, in the emergence order, we were only able to assess the last part of this activity transition as we could not observe individual movements below ground. Similarly, in the leaving order, even if we recorded all individual movements, we only analysed the initiation which all individuals joined (i.e., the last one before the group started foraging). We therefore believe that comparing these two contexts under a leadership framework makes biological sense.

(e) ***Effect of weight change***

At the KMP, meerkats were used to be weighted three times a day by voluntary entering a tray fixed on electronic scales (Clutton-Brock et al., 1999a). The tray was baited with small crumbles of boiled eggs and a few drops of water were also rewarded after weighing. To assess the effect of weight change on the emergence order and on the leaving order, we calculated weight changes over 6 specific periods for each meerkat in a group: the previous morning weight change (PMFS, eq. 2), the previous day weight change (PDFS, eq. 3), the previous night weight change (PNWL, eq. 4), the previous morning to actual morning weight change (PMAMFS, eq. 5), the actual morning weight change (AMFS, eq. 6) and the actual day weight change (ADFS, eq. 7). The weight changes are relative for each individual since its considered weight change is divided by its initial weight. Because mainly adults are emerging or leaving first, we restricted the analysis to adult individuals (i.e., all days when non-adults emerged or left first were discarded).

(2) PMFS = (PLW - PMW) / PMW

(3) PDFS = (PEW - PMW) / PMW

(4) PNWL = (AMW - PEW) / PEW

(5) PMAMFS = (AMW - PMW) / PMW

(6) AMFS = (ALW - AMW) / AMW

(7) ADFS = (AEW - AMW) / AMW

where PMW is the previous morning weight (before the meerkats start foraging), PLW the previous lunch weight (after approximately 3 hours of foraging), PEW the previous evening weight (after the meerkats stopped foraging for the day), AMW the actual morning weight, ALW the actual lunch weight and AEW the actual evening weight (all weights are measured in grams). Then, meerkats were ranked according to their weight change and equation (1) was used to standardise the weight change from 0 (best weight change) to 1 (worst weight change).

With data from the KMP long-term database, we analysed the average weight change rank of the first individual up (the only individual for which we have its position in the emergence order). If weight change ranking had an influence on the identity of the first individual up, then its average weight change rank would differ from 0.5. A significantly smaller value than 0.5 would mean that successful foragers tend to emerge first. Conversely, a significantly greater value than 0.5 would mean that less successful foragers tend to emerge first. With our own data collected in the field, we recorded all the individuals' leaving order. We can therefore test the correlation between leaving order and weight change ranking.

(f) ***Effect of previous babysitting***

To test the effect of babysitting on the previous day on emerging first or leaving first, we checked the long-term database for individuals recorded as babysitting in both sessions (morning and evening) of the day prior to the day of interest. This was to ensure that babysitters had suspended foraging activity for a considerably long period. Therefore, previous babysitters should be hungrier than other group members.

(g) *Repeatability*

The repeatability is the intraclass correlation coefficient and its calculation is derived from a table of a one-way analysis of variance (ANOVA). Therefore, a behaviour is repeatable when the variance among individuals is higher than the variance within individuals (Lessells & Boag, 1987). We calculated the repeatability of the ratio of the observed frequency to the expected frequency of emerging first. The observed frequency of being first up was determined by dividing for every month the number of times an individual was first up by the number of visits to the group when this individual was present on that month (we included only months in which the individual was present at least five times). The expected frequency of being first up was calculated by averaging the reciprocal of the number of adults present in the group (when the relevant individual was present) on each visit over each included month. Therefore, a ratio of 0 means that the individual has not been observed to emerge first during that month; whereas a ratio of 3 means that the individual emerged first 3 times more often than expected.

(h) *Statistical analysis*

Tests for the study of activity transitions were done using SPSS 16.0 for Windows (SPSS Inc., Chicago, IL, USA). To analyse the effect of age, sex, female's reproductive status, social status and babysitting, we compared the expected values (which are the proportions of the relevant categories within the group) to the observed values (which are the actual proportions of each relevant category seen emerging first) for the emergence of the first individual without averaging per month by conducting exact Wilcoxon signed-rank tests. For the analysis of foraging success, we conducted a t-test to compare the sample of foraging success values we had to the expected value of 0.5 if foraging success had no influence on emerging first. Calculations for the repeatability analysis have been done in Excel 2003, following the procedure of Lessells & Boag (1987). Correlations between rank orders were analysed with the Spearman's rank correlation test (Barelli et al., 2008) for each morning. We then tested whether the correlation coefficients calculated for each group were significantly different by using an appropriate χ^2 calculation (Zar, 1999). If this test was not significant, we then calculated the common correlation coefficient for each group (Zar, 1999). Finally, we tested these common correlation coefficients to assess whether it was significantly different from 0 by using an appropriate Z calculation

(Zar, 1999). In addition, we conducted specific analyses for 4 categories of individuals: the first individual up, the last individual up, the individuals in the first half of the emergence order and the individuals in the second half of the emergence order. We tested whether being part of these categories had an influence on the leaving order (i.e., whether the first individual up was more often in the first half of the leaving sequence, for instance). Such an influence would be reflected by an average leaving order different from 0.5 (smaller if belonging to the relevant category increases the probability of leaving early and larger if belonging to the relevant category increases the probability of leaving late). We therefore conducted a t-test to compare the sample of leaving order ranks to the expected value of 0.5 if the emergence order had no influence on the leaving order for each of the 4 categories.

3. RESULTS

(a) *Emergence order*

Effect of age, status and sex

Age category had a significant effect on the probability of being first up, with adults almost exclusively emerging first (exact Wilcoxon signed-rank tests; N = 13 groups for all categories; Pup: $Z = -3.18$, $p < 0.001$; Juvenile: $Z = -3.18$, $p < 0.001$; Sub-Adult: $Z = -3.18$, $p < 0.001$; Adult 1: $Z = -2.62$, $p < 0.01$; Adult 2: $Z = -3.18$, $p < 0.001$; Figure 1). Within adults, we did not find a higher probability for older individuals to emerge first (exact Wilcoxon signed-rank tests; all $p > 0.05$; Figure 2). Social status also had no effect on the probability of emerging first (exact Wilcoxon signed-rank tests; Dominant: $Z = -0.39$; Subordinate: $Z = -1.33$; N = 12 groups for all tests, as one group did not fulfil the conditions; all $p > 0.2$). Sex did not have an effect on the probability of emerging first during the non-breeding season, nor during the reproductive period (exact Wilcoxon signed-rank test; N = 13 groups for all tests; Non-breeding season: $Z = -0.31$; Pregnancy: $Z = -1.08$; Lactation: $Z = -1.29$; all $p > 0.2$). Some individuals were emerging first far more often than expected whereas other individuals never emerged first, and this trait holds true throughout the individuals' adulthood (as we have seen that mainly adults emerged first, we restricted the analysis to this age category). Indeed, we found highly significant repeatability for every group investigated (N = 5 groups, Figure 3 & Table 1).

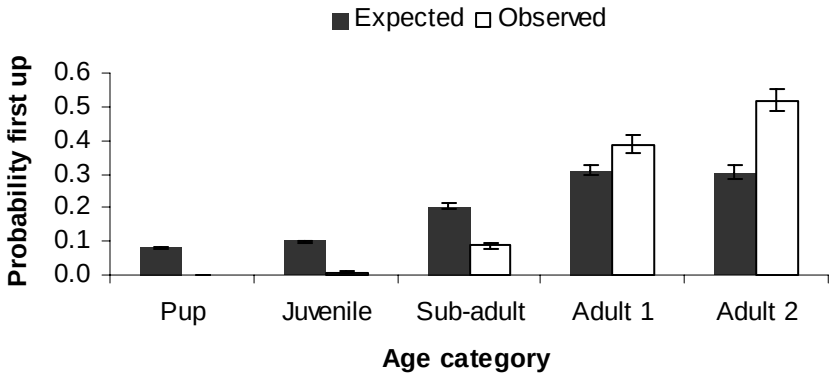

Figure 1. Effect of age category on the probability of emerging first. Pup: 0-3 months; Juvenile: 3-6 months; Sub-adult: 6-12 months; Adult 1: 12-24 months; Adult 2: >24 months. Mean ± se. N = 13 groups.

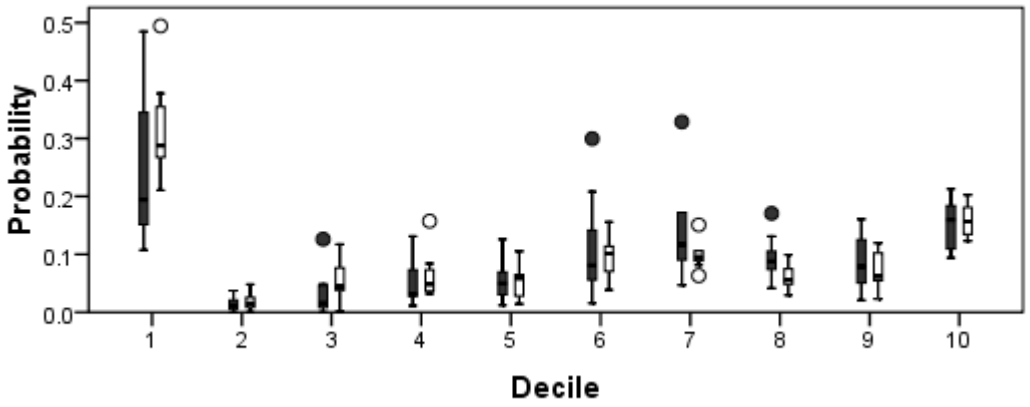

Figure 2. Probability of an individual to emerge first depending on its relative age in a group. Observed (dark grey) and expected (white) probabilities of emerging first for the 10 deciles of adult members of a meerkat group. An adult belongs to the first decile of its group when it is among the 10 % of the youngest members of the group. It belongs to the tenth decile when it is among the 10 % of the oldest members of the group. For the box-plots, thick lines show the median, the bottom and top of the box represent the first and the third quartiles respectively. Limits of the whiskers represent minimum and maximum values of the data, without outliers. Circles represent outliers, which are more than 1 interquartile range from the end of the box. N = 9 groups.

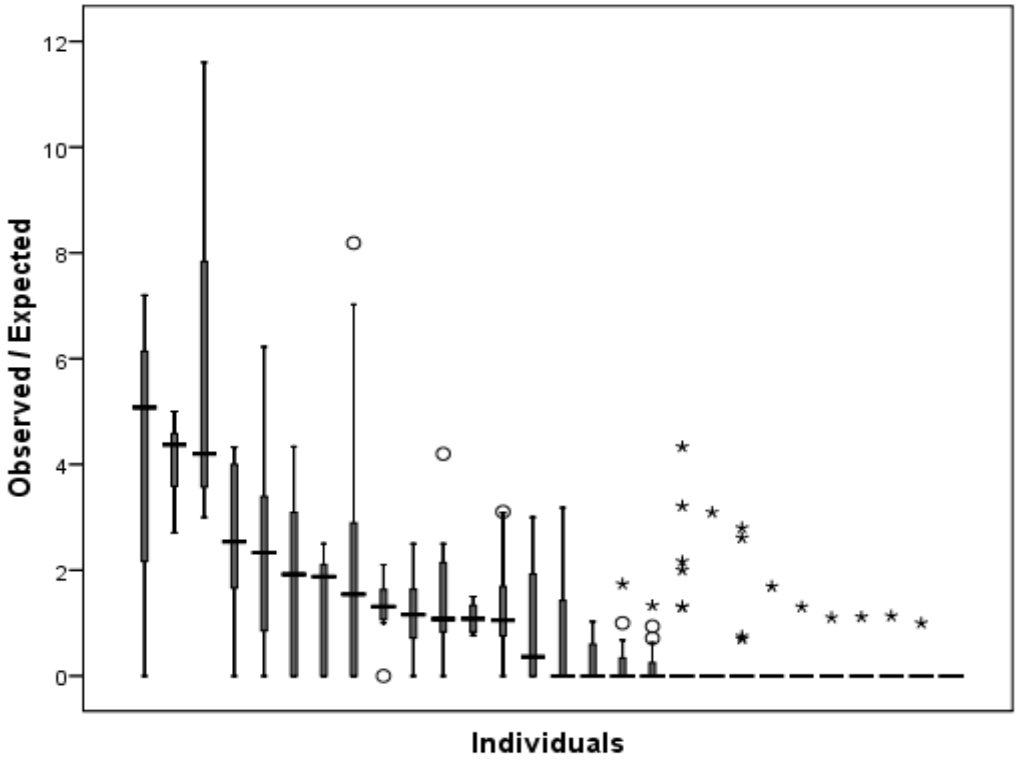

Figure 3. Boxplots of the observed-to-expected ratio of emerging first for a group of 28 adult meerkats. Thick bars represent the median, the bottom and top of the box represent the lower and the upper quartiles, respectively. The whiskers represent the limits of the 95 % confidence interval. Circles and stars represent outliers. Individuals are ordered by decreasing median values.

Table 1. Repeatability of propensity of emerging first.

Group	n_0	*F* ratio (df)	p^a	Repeatability
Balrog	11.55	8.314 (10,119)	***	0.388
Commandos	13.57	18.792 (22,292)	***	0.567
Drie Doring	10.94	10.865 (27,282)	***	0.474
Elveera	14.26	8.933 (67,908)	***	0.358
Frisky	12.02	7.850 (63,709)	***	0.363

***: $p < 0.001$

Effect of previous day's foraging success on emerging first

The previous day's foraging average rank of the individual emerging first did not differ significantly from 0.5 (which means an individual with an average foraging success), with values covering the whole range of possible values, from 0 to 1. This was true for all the different measures of foraging success. Therefore, foraging success did not influence the probability of emerging first (t-tests; PMFS: $t_7 = 1.71$, $p = 0.13$; PDFS: $t_7 = -1.23$, $p = 0.26$; PNWL: $t_8 = -0.39$, $p = 0.71$; PMAMFS: $t_7 = -0.80$, $p = 0.45$). Babysitters of the previous day were not more likely to emerge first on the day of interest than other individuals (exact Wilcoxon signed-rank test, $Z = -1.02$, N = 12 as one group did not have enough babysitting events, $p = 0.34$).

(b) *Leaving order*

Effect of age, status and sex

Adult individuals initiated the leaving process more frequently than expected, contrary to the other age categories (exact Wilcoxon signed-rank tests; N = 11 for all categories; Pup: $Z = -2.20$, $p < 0.05$; Juvenile: $Z = -2.81$, $p < 0.01$; Sub-Adult: $Z = -2.20$, $p < 0.05$; Adult 1: $Z = -0.25$, NS; Adult 2: $Z = -2.41$, $p < 0.05$). There was no difference in the probability of leaving the burrow first between dominants and subordinates (exact Wilcoxon signed-rank test; N = 7; $Z = -0.51$; $p > 0.6$). Outside the breeding season, sex had no effect on leaving order (exact Wilcoxon signed-rank test; N = 11; $Z = -0.09$; $p > 0.9$; Figure 4A). Within the breeding season, males were more likely to lead the group away during the "Pregnancy" period (exact Wilcoxon signed-rank test; N = 10; $Z = -2.31$; $p < 0.05$; Figure 4B), and lactating females always left first during the "Lactation" period (exact Wilcoxon signed-rank test; N = 5; $Z = -2.03$; $p = 0.06$; Figure 4C). In the non-breeding season (during which sex had no effect), for 51 days of observations over 7 groups, we had only 19 different individuals recorded as emerging first while we had 35 different individuals recorded as leaving first for these same days. Therefore, leaving first seemed to be less repeatable among individuals than emerging first.

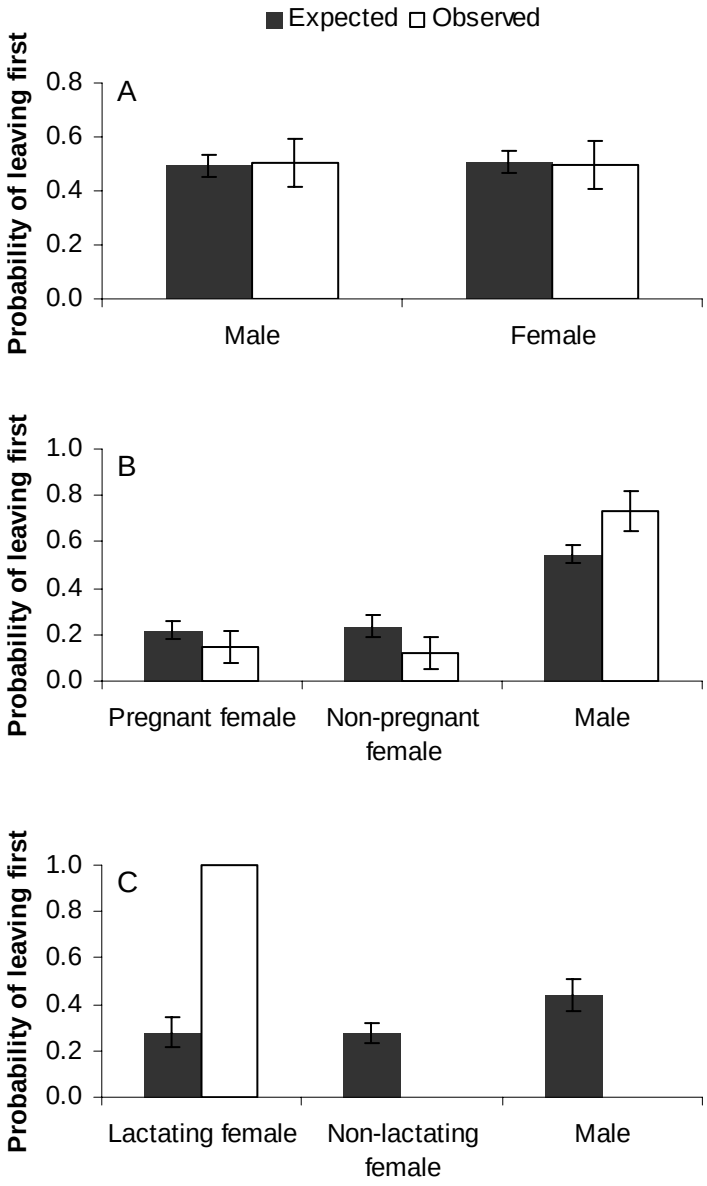

Figure 4. Effect of sex on the probability of leaving the burrow first. A) non-breeding season (N = 11 groups); B) during pregnancy periods (at least one pregnant female present in the group, N = 10 groups); and C) during lactation periods (at least one lactating female present in the group, N = 5 groups). Only adults were included. Mean ± se.

Effect of previous day's foraging success on leaving first

Foraging success of the overall previous day was negatively correlated with leaving order on the next morning (PDFS: Pearson's r = -0.232, N = 97, $p = 0.022$; Figure 5), but leaving order was not correlated to any other measures of foraging success: PMFS (Pearson's r = -0.104, N = 175, $p = 0.17$), PNWL (Pearson's r = 0.203, N = 64, $p = 0.06$), AMFS (Pearson's r = -0.036, N = 96, $p = 0.73$) and ADFS (Pearson's r = 0.158, N = 55, $p = 0.25$). There was no evidence that babysitting on the previous day increased the probability of leaving first on the day of interest (exact Wilcoxon signed-rank test, $Z = -0.17$, N = 7, $p = 0.94$).

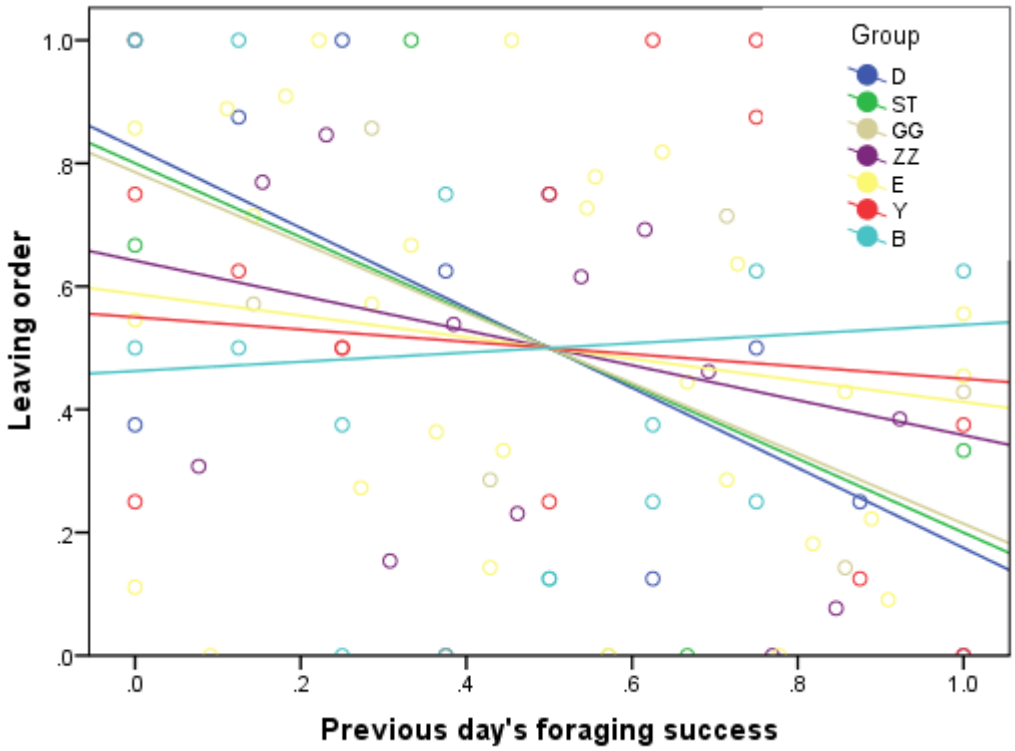

Figure 5. Correlation between the previous day's foraging success of an individual and its leaving order on the day of interest for 7 meerkat groups. Previous day's foraging success score varies from 0 (best foraging success) to 1 (worst foraging success). Leaving order score varies from 0 (first individual to leave) to 1 (last individual to leave).

(c) *Correlation between emergence order and leaving order*

For 3 out of the 11 groups investigated, there was a positive correlation between the position a meerkat had in the emergence order with its position in the leaving order (GG, ST and E, all *p*-values < 0.05, Figure 6). No other groups differed significantly from a null correlation between emergence order and leaving order. The first individual up did not differ from an average leaving order (0.419 ± 0.073, range: 0.000 – 0.846, N = 13, t_{12} = -1.106, p = 0.29), neither did the last individual up (0.614 ± 0.067, range: 0.077 – 1.000, N = 13, t_{12} = 1.714, p = 0.11). However, individuals in the first half of the emergence order were more often in the first half of the leaving order (0.444 ± 0.018, range: 0.317 – 0.5714, N = 13, t_{12} = -3.062, p = 0.01). Symmetrically, individuals in the second half of the emergence order were more often in the second half of the leaving order (0.5578 ± 0.0226, range: 0.429 – 0.720, N = 13, t_{12} = 2.558, p < 0.05).

4. DISCUSSION

Before starting foraging in the morning, meerkat groups face two activity transitions. During the first one, meerkats venture outside of their underground burrow. Adults typically emerged first and individual differences in emergence order were not related to any of the characteristics that we investigated, including sex, social status, female's reproductive state, foraging success, and previous babysitting. However, some individuals repeatedly emerged first more often than expected. The observed regularity through time is a pre-requisite of a personality trait, which describes behavioural differences "consistent over time and context" (Stevenson-Hinde, 1983; Kurvers et al., 2009). Emerging first might allow the first individual up to assess the relative safety of the surroundings before other individuals emerge as well. If emerging first truly reflects a vigilant personality trait, individuals emerging first should also be the individuals showing higher vigilance behaviour while foraging. Even though vigilance in meerkats is influenced by nutritional constraints (Clutton-Brock et al., 1999b), it is interesting to note that some individuals contribute disproportionally more than others to vigilance (KMP, unpublished data). On the other hand, the consistency of individuals emerging first might also help to better understand the mechanisms underlying multi-generational persistence of emerging behaviour (Thornton et al., 2010). Yet, this consistency could simply be explained by

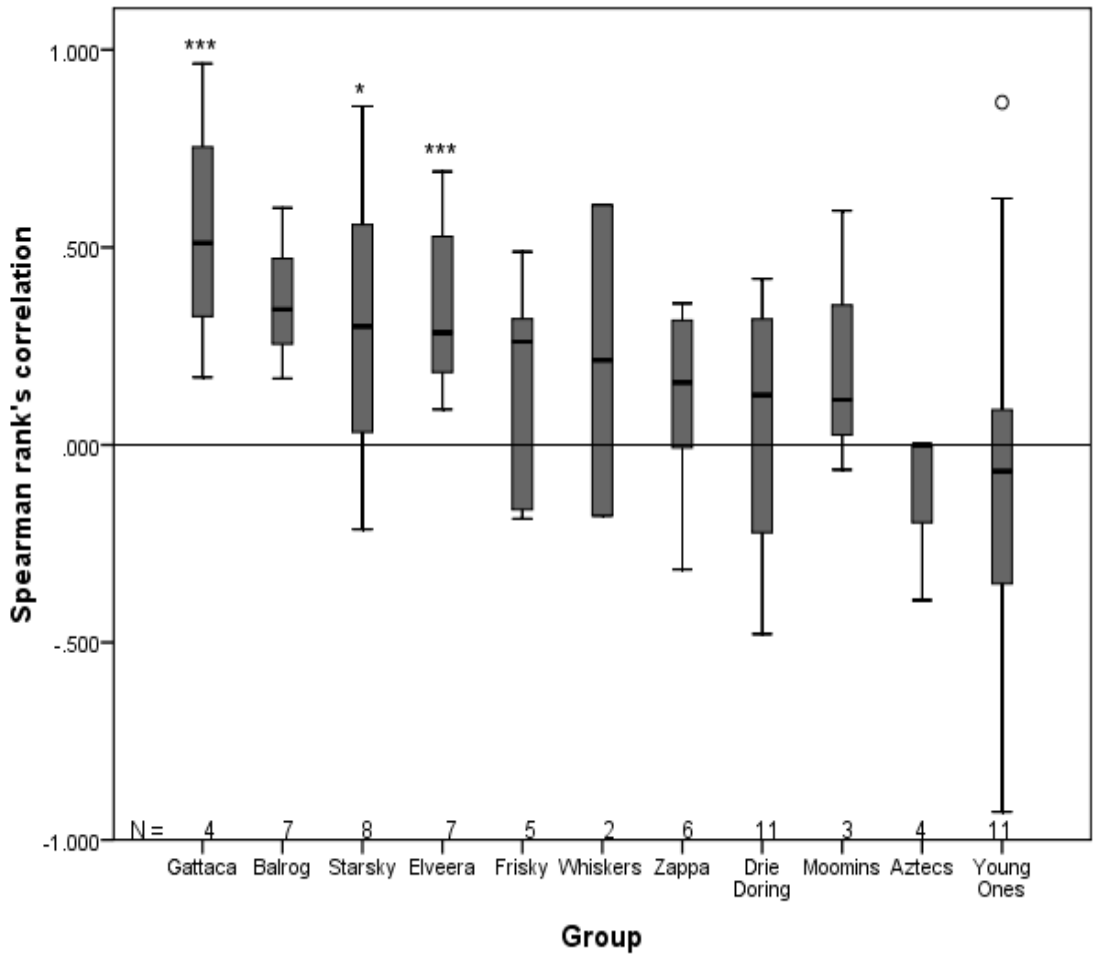

Figure 6. Boxplots of the correlation coefficients between emergence and leaving order obtained for 11 meerkat groups. Thick bars represent the median, the bottom and top of the box represent the lower and the upper quartiles, respectively. The whiskers represent the limits of the 95 % confidence interval. Circle represents an outlier. N represents the number of mornings for which a correlation has been computed. Asterisks indicate statistical differences from a null correlation coefficient: * for $p < 0.05$, and *** for $p < 0.001$.

the physical constraints of the underground burrow galleries. Even though it was impossible to directly assess this effect in our protocol, it seems unlikely that it could explain the observed pattern, mainly because meerkat burrows contain several independent "chambers" where meerkats sleep and because the galleries are wide enough to allow crossing of individuals (C. Bousquet, pers. obs.).

During their second activity transition, meerkats leave their burrow to start foraging. The leaving order was more equally distributed among adult group members

and more strongly influenced by physiological needs: the previous day's foraging success and the reproductive state of females were good predictors of an individual's propensity to lead. Outside the breeding season, unsuccessful foragers left the burrow first and were followed by the rest of the group, which made them "leaders" (in the sense of King, 2010). During breeding periods, other factors interfered with foraging success. First, males led more often than females when pregnant females were present in their group. These early leaving males are likely to be rover males, who temporarily leave their group to prospect for mating opportunities in other groups (Young et al., 2005). Therefore, in this period, males have a higher incentive than females to leave. Yet, the roving incentive is offset by the physiological requirement of lactating females. Indeed, once lactating females were in the group, they were always found to lead the group. Our results in combination with previous studies highlight the concept that physiological needs are an important predictor of leading behaviour (Rands et al., 2008; Conradt et al., 2009). However, we also found that former babysitters did not lead the group more often than expected. This contrasts with the "physiological needs" hypothesis. One potential explanation could be that lactation and unsuccessful foraging are more physiologically demanding than babysitting. Surprisingly, the earlier propensity of needier individuals to leave the burrow did not affect subsequent foraging success, as even next morning foraging success was not higher for individuals leaving first. It might be that leaving first provides only an immediate foraging benefit, which we did not detect when we weighed the meerkats 3 hours afterwards.

It is becoming more and more understood that group activity transitions consist of a continuum of individual movements (Petit & Bon, 2010). However, the last part of this continuum (i.e., the last movements of each individual leading to the actual activity transition) can still reveal the pivotal role of certain factors or of certain individuals in the group decision process (King, 2010). Here, we showed that this last part of the continuum can be under the influence of different variables in two different contexts: individual identity was prevalent for the emergence order while foraging success negatively correlated with leaving order.

Overall, the differences in organization of morning activity transitions can help to understand the absence of correlation between emergence order and leaving order. Intrinsically more vigilant individuals could make transitions between safe and more exposed environments while physiological constraints could push individuals to

initiate transitions between resting and foraging. In both situations, consensus costs would be minimised by a different type of leadership. In risky transitions, costs would be reduced by the unshared leadership of a more vigilant or informed individual (Lusseau & Conradt, 2009). In foraging transitions, costs would be reduced by not necessarily conscious turn-taking among individuals facing physiological needs to lead (Harcourt et al., 2010). With this in mind, more research on experimental and observational comparisons of leadership in different natural contexts needs to be carried out in a wide range of species to identify all the causes of leadership and to deepen our understanding of the relationship between activity initiation and leadership.

5. ACKNOWLEDGMENTS

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CHAPTER 2

Sleeping Burrow Renovation in Meerkats (*Suricata suricatta*): a Socially Facilitated Group Behaviour

To be submitted

Sleeping Burrow Renovation in Meerkats (*Suricata suricatta*): a Socially Facilitated Group Behaviour

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To be submitted

Summary

Coordination of behaviours among group members in social groups can be reached *via* two mechanisms. The behaviour of an initiator can either spread through the group *via* social facilitation or *via* active recruiting with specific signals. Signalling enables individuals to stop constantly monitoring other group members' behaviours directly and save time and energy for other activities. However, signalling is more cognitively demanding to process. Evolutionarily, there is therefore a trade-off between the cognitive requirements of the signal and the importance of coordination for group members. We analyzed the burrow renovation behaviour of meerkat groups when they were stationary at their burrow. Renovation was mainly done by single individuals and we did not detect signals associated with this activity. Yet, on mornings with more renovators, groups renovated longer than expected. This increased contribution in renovation may be explained by social facilitation. The lack of signalling for burrow renovation is likely to reflect the unimportance of precise coordination of burrow renovation among meerkat group members, rather than a cognitive limitation of meerkats to process an additional signal to their already relatively large repertoire.

Keywords: stationary groups; signalling; social facilitation; meerkat

1. INTRODUCTION

Animals in their daily activities constantly face choices between mutually exclusive actions, and in social groups these have to be coordinated with other group members. Such coordination can be reached either by social facilitation (when an individual's probability to choose an activity increases with the number of other group members already doing this activity; Zajonc, 1965; Clayton 1978) or by the use of specific signals (Prins, 1996; Bousquet et al., 2011). Coordination *via* social facilitation requires that an individual detects the behaviour of another individual and then adopts this behaviour (Clayton, 1978). On the other hand, coordination *via* signalling requires that an individual detects the signal emitted by another individual performing a behaviour and then adopts this behaviour (Endler, 1993). Signalling has therefore the advantage of freeing the receiver from constantly monitoring the behaviour of the emitter. However, processing signals is more cognitively demanding (Endler, 1993). Therefore, the evolution of coordination *via* signalling is the result of a trade-off between (i) the ease of monitoring others' behaviours, (ii) the cognitive requirements for the processing of the putative signal and (iii) the importance of coordination at the group level for the task under selection. Signals for group coordination have been found in situations in which a group risks fragmentation (i.e. when changing location; Prins, 1996; Bousquet et al., 2011) or in which group efficiency is highly affected by coordination (i.e. food harvest in ants *via* trail pheromone; Camazine et al., 2001).

In the morning or in the evening, many social living species spend time close to their sleeping sites in their natural habitat (Reichard, 1998). During these periods, social groups can engage in various activities while remaining in the same location. Meerkats, a species of group-living mongoose in southern Africa (Doolan & Macdonald, 1996), use their time near their sleeping burrow to engage in many social interactions such as allogrooming or dominance displays (Kutsukake & Clutton-Brock, 2006; Madden et al., 2009). Besides such interactions, meerkats also renovate their sleeping burrow entrances during this period (Clutton-Brock et al., 2002). Meerkats use a large number of burrow systems throughout their home range (Manser & Bell, 2004). Typically, meerkat groups change burrows several times a week, except during the babysitting period (as long as pups and a few adult babysitters remain at the burrow while the rest of the group is foraging) when they stay at the same burrow for up to four weeks (Clutton-Brock et al., 2000). The duration of

burrow renovation in meerkat groups varies greatly from day to day (from no renovation up to 30 minutes) and individuals vary in their contribution depending on social status and sex (Clutton-Brock et al., 2002; Clutton-Brock et al., 2004). However, little is known about how meerkats organize their burrow renovation bouts at the group level.

We investigated the coordination of sleeping burrow renovation, a behaviour that has been described as a cooperative activity in meerkats (Clutton-Brock et al., 2002). We first assessed the biotic and abiotic factors favouring or inhibiting renovation in meerkats. Then, we determined whether a specific signal was associated with this behaviour. As no signal was found, we determined whether renovation was socially facilitated. We then discuss why no signal evolved to coordinate renovation activity at the group level.

2. MATERIALS AND METHODS

(a) *Study site and population*

We studied sleeping burrow renovation in meerkats on the wild but habituated population of the Kalahari Meerkat Project on ranchland in the South African Kalahari, near Van Zylsrus (26° 58' S, 21° 49' E). Descriptions of habitat and climate are provided elsewhere (Clutton-Brock et al., 1999; Russell et al., 2002). At least one individual in each meerkat group is fitted with a radio transmitter (Sirtrack, Havelock North, New Zealand), allowing us to locate it at any time during the day (Jordan et al., 2007; Golabek et al., 2008). All animals in the population could be individually identified by the use of unique dye mark combinations. Individuals were habituated to close observation (< 1 m), facilitating the recording of the individuals' identity and of the precise duration of behavioural bouts (to the second). The ages of over 95 % of individuals were known precisely (± 5 days) as well as most of their life-history events.

For this study, data were collected between August 2006 and March 2007 on 8 groups. Group size varied from 5 to 17 individuals (average: 11.3 ± 1.0), including in total over 90 individuals. We quantified renovation behaviour during more than 40 group-hours (9 to 13 mornings per group) of observation when meerkats were at their burrow before leaving for foraging (we only considered morning burrow renovation). Due to birth, death, evictions and roving events, group sizes of each focal group

changed during the observation period (minimal change: no individuals, maximal change: five individuals).

(b) ***Ecological conditions favouring burrow renovation***

We were interested in the influence of the following explanatory variables on the group renovation process: i) Weather: factor with two levels (Overcast or Fine); ii) Wind: factor with two levels (Presence or Absence); iii) Sand quality: factor with two levels (Soft or Hard); iv) Time spent at the burrow: factor with three levels (≤ 19 min, 20-31 min or ≥ 32 min); v) Days of use: factor with two levels (< 2 days or ≥ 2 days); vi) Group identity: factor with eight levels (one for each studied group); vii) Return: factor with two levels (Return or No return).

We tested for correlations between these explanatory variables. Only two variables were correlated: "Group identity" and "sand quality". Both variables are correlated because some groups lived on territories with only hard sand burrows and some other groups lived on territories with only soft sand burrows. However, most of the groups had a mixture of sand quality burrows. We decided to keep both variables in the models at the beginning of the simplification process.

To determine which factors influenced morning burrow renovation in meerkats, we fitted several models until reaching a minimal adequate model by stepwise processes in R 2.10.0 (R development core team, 2009). For the probability of renovation, we used generalised mixed-effect models with quasibinomial error distribution and group identity as a random term. For the duration of renovation, we used generalised mixed-effect models with a Gamma error distribution (because the data was skewed towards small values of duration) and group identity as a random term.

(c) ***Consistency of contribution to sleeping burrow renovation***

When meerkats were renovating, we systematically recorded who renovated and for how long. First, by summing all individual durations, we calculated the group's renovation effort for each morning. Second, on mornings when groups renovated, we checked whether specific classes of animals were responsible for the observed group pattern. The following variables were used: age (Pups: < 3 months old, Juveniles: 3 to 6 months old, Sub-adults: 6 to 12 months old, Adults 1: 12 to 24 months old and Adults 2: > 24 months old), sex (Males and Females) and

social status (Dominants and Subordinates). To assess the effect of these variables, we conducted generalized linear mixed-effect models. Date of observation and individual nested within group were entered as random terms. The duration of renovation was following a quasipoisson distribution. To test the fixed effects, we added all three variables and all random terms in the initial model, fitted by the maximum likelihood method. Then, we removed a focal variable from the initial model. The model without the focal variable was then tested against the full model by performing an ANOVA between the two models. The level of significance of the ANOVA gives the level of significance of the focal variable. To test the random terms, we added all three variables and all random terms in the initial model, fitted by the restricted maximum likelihood method. Random terms were then tested by ANOVAs between the initial model and the model without the focal random term. The final minimal model is the model containing all the variables and the random terms which were significant at the level $\alpha = 0.05$.

We tested the consistency of individuals in renovation behaviour by calculating its repeatability. A behaviour is considered repeatable when within-individual variation is low and/or between-individual variation is large (Lessells & Boag, 1987; Nakagawa & Schielzeth, 2010). We assessed the repeatability of renovation behaviour by first measuring for each sub-adult and adult its ratio "observed" to "expected" (equal contribution by all present sub-adult and adult members) renovation duration over at least 5 mornings during which its group renovated. We then conducted an ANOVA of this ratio in function of individual's identity to determine the level of repeatability and its significance (Lessells & Boag, 1987; Nakagawa & Schielzeth, 2010).

(d) *Coordination* via *social facilitation or* via *signalling?*

To determine whether coordination of sleeping burrow renovation in meerkats is reached *via* social facilitation or *via* signalling, we first determined whether we could detect any acoustical or visual signals (other than renovation behaviour itself) associated with renovation behaviour. Then, we assessed the duration of group renovation according to the number of individuals involved. Furthermore, we were interested in the marginal contribution of new contributors. To do so, we took as the reference the average renovation duration in mornings during which only one individual was renovating: $ave_{(1)} \pm se_{(1)}$, where $ave_{(1)}$ is the average value for one

individual and $se_{(1)}$ the standard error of the mean for one individual. If there was no interaction between renovators (no social facilitation), we expected N individuals renovating in the same morning to renovate N times as long as lonely renovators. To be conservative, we calculated the expected value for N individuals involved in renovation ($exp_{(N)}$) as N times the maximum value of the 95 % interval of the mean for one individual:

$$exp_{(N)} = N * (ave_{(1)} + 1.96 * se_{(1)}) \quad (1)$$

We then determined how much renovation excess there was on average for each individual by dividing the difference between the observed and the expected value by the number of individuals involved. In the case of N individuals involved, the individual renovation excess is given by equation 2:

$$rex_{(N)} = (obs_{(N)} - exp_{(N)}) / N \quad (2)$$

where $rex_{(N)}$ is the renovation excess for each of the N individuals involved and $obs_{(N)}$ is the average observed duration of renovation for N individuals.

3. RESULTS

(a) *Contribution of different group members to burrow renovation*

Age, sex and social status affected the contribution to burrow renovation and this was consistent over time at the individual level. The three variables integrated as fixed effects in the full generalized mixed-effect model were significant (Table 1): adults more than 1 year-old renovated longer than pups, juveniles and sub-adults, males renovated longer than females and dominants renovated longer than subordinates. Thereby, individuals were consistent through time in their renovation behaviour. The ratio of observed duration to expected duration was significantly repeatable ($r = 0.1803 \pm 0.0421$, $p < 0.001$). The relatively low absolute value of repeatability can be explained by the fact that renovation is overall a rare behaviour in meerkats.

Table 1. GLMM with quasipoisson family of renovation duration. χ^2, d. f. and *p* are the result, the degrees of freedom and the corresponding probability of the ANOVA between the model without the effect of interest and the full model, respectively.

Fixed effects	χ^2	d. f.	*p*
Age	407.19	4	< 0.001
Sex	5.58	1	< 0.050
Social status	190.49	1	< 0.001
Random effects			
Date	17644	1	< 0.001
Individual	15217	1	< 0.001
Group	0.09	1	0.760

(b) ***Ecological conditions influencing burrow renovation***

"Wind" and "Sand quality" were the only two factors affecting the renovation probability. The absence of wind increased the probability that meerkats would renovate their burrow, while there was a tendency for meerkat groups to renovate more often when they used soft sand burrows (Table 2).

"Sand quality" and "Days of use" affected the renovation duration, whereas the five other factors did not have an influence. Meerkats spent more time renovating when the sand was soft and when the group arrived recently at the burrow (Table 3).

Table 2. ANOVA table of the minimal adequate model for renovation probability.

Factor	SS	d. f.	MS	F	*p*
Sand	3.140	1	3.140	2.617	0.0764
Wind	7.570	1	7.570	6.308	0.0059
Error	71.982	60	1.200		
Total	82.692	62			

Table 3. ANOVA table of the minimal adequate model for renovation duration.

Factor	SS	d. f.	MS	F	*p*
Sand	6.289	1	6.289	3.654	0.0122
Days of use	6.201	1	6.201	3.603	0.0128
Error	63.683	37	1.721		
Total	76.173	39			

(c) *Organization*

Digging bouts involving only one individual were much more frequent than bouts involving several individuals (single: 8.03 ± 1.62; several: 1.75 ± 0.38 bouts per morning, exact Wilcoxon signed-rank test: N = 7, $V = 36$, $p = 0.008$, Figure 1). Furthermore, the duration of renovating bouts involving only one individual alone (21.06 ± 3.09 s) was longer than the time spent renovating by an individual before another meerkat joined in a shared renovation bout (13.12 ± 2.00 s; GLMM with quasipoisson distribution and individuals nested within groups as random terms, $\chi^2 = 208.78$, d.f. = 1, $p < 0.001$, Figure 2). Therefore, the higher number of renovation bouts by single individuals was not due to a lack of time for joiners to join in.

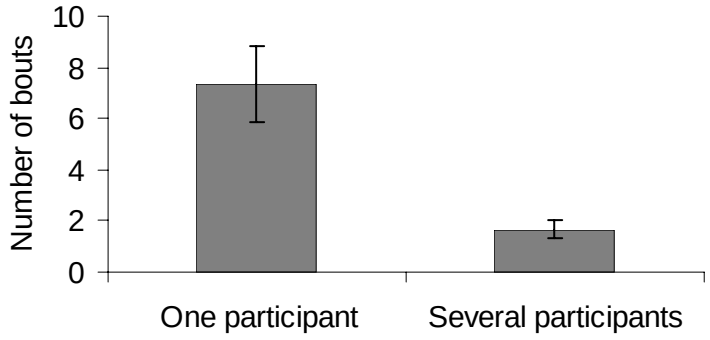

Figure 1. Number of renovating bouts (mean ± s. e.; N = 8 groups) made by only one individual or several individuals per morning in which renovation occurred.

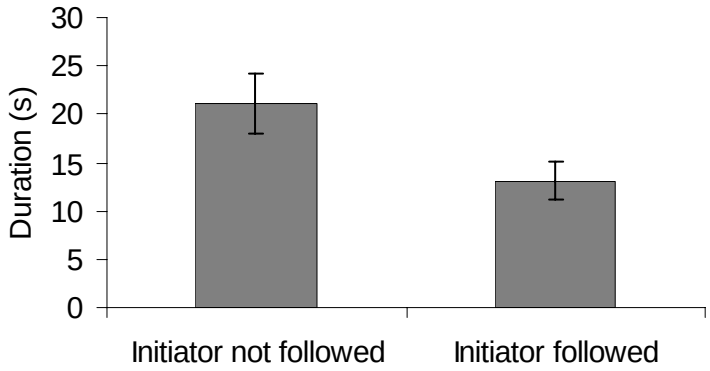

Figure 2. Duration (mean ± s. e.; N = 8 groups) of renovation until an initiator was followed or not. If the initiator was not followed, the duration equalled the total duration of the bout. If the initiator was followed, the reported duration was the duration until the first joiner began to follow.

(d) ***Group renovation increased with the number of involved individuals***

We never observed any obvious visual or acoustic signal associated with group renovation. However, duration of group renovation increased linearly with the number of individuals involved ($r^2 = 0.93$). On mornings when only one individual was renovating, the overall renovation duration was 22.6 ± 3.3 s (N = 8 groups). Thus, according to equation (1), the expected value for two individuals equals: 58.1 s [$exp_{(2)} = 2 * (22.6 + 1.96 * 3.3)$]. The observed value when two individuals were digging was 130.1 ± 83.4 s (N = 6 groups). Therefore, according to equation (2), the renovation excess for each of the two individuals equals 36 s [$rex_{(2)} = (130.1 – 58.1) / 2$]. The discrepancy between observed and expected values increased with the number of individuals involved (Spearman's rho correlation, r = 0.829, $p = 0.042$, N = 6, Figure 3A) and with the proportion of group members involved (Figure 3B).

4. DISCUSSION

The absence of a specific signal and the temporal aspect of how burrow renovation is distributed among meerkats indicates that the coordination of this group activity is reached *via* social facilitation and not *via* signalling. Age category, sex and social status of an individual affected the renovation duration of an individual. Despite these effects, there were consistent differences between individuals, whereby few of them contributed substantially more and several did not contribute at all or only a little, and this was consistent over the days. Meerkats were rarely seen renovating at the same time in the same entrance. However, the individual contribution of each meerkat increased with the number of individuals involved.

The analysis of temporal organization revealed that burrow renovation was mainly a solitary task, as renovation bouts made by only one individual were about 4.5 times more frequent than bouts made by several individuals. This was not because solitary renovators did not renovate long enough to recruit other individuals. It was rare to see all the adults of any group participating at the same time or during the same morning in burrow renovation (Christophe Bousquet, pers. obs.). However, the number of individuals involved in the renovation process influenced an individual's renovation duration. The greater the number of individuals that were involved, the longer each individual renovated. For instance, when two individuals were involved, the total duration was about 70 seconds longer (130 s against 58 s) than the expected

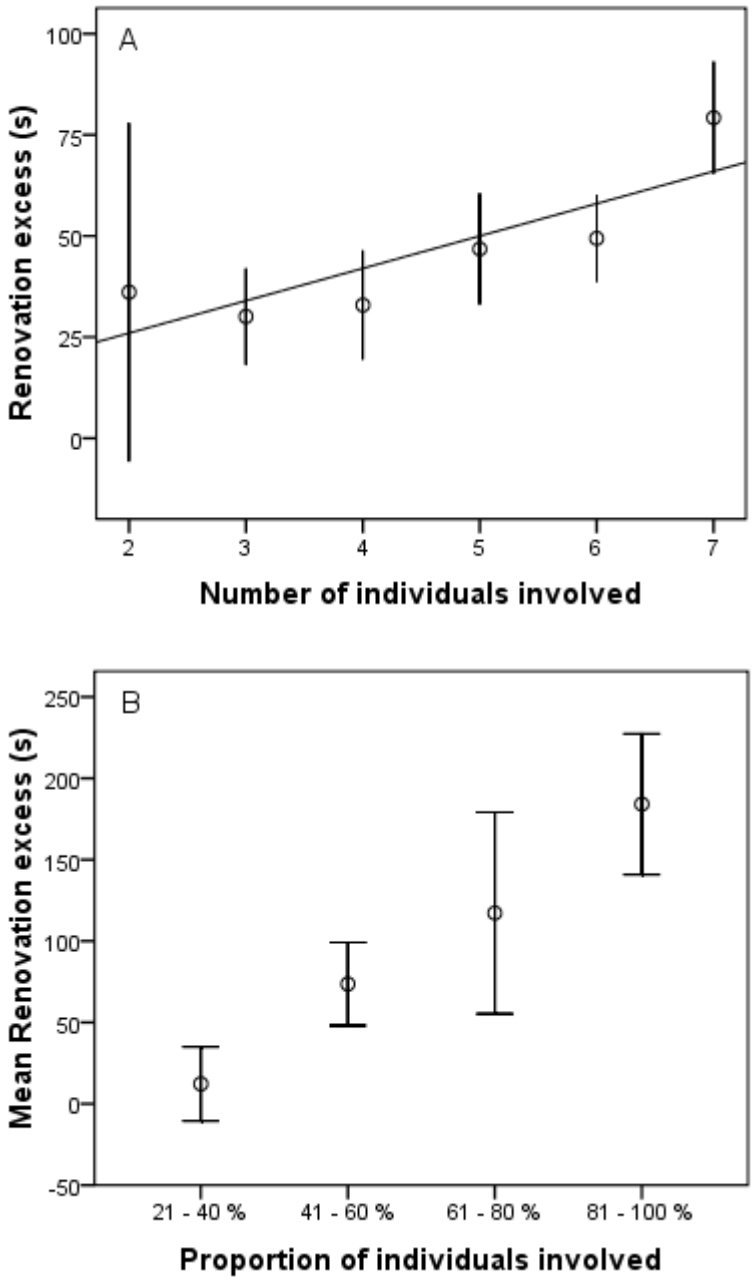

Figure 3. Renovation excess (s) from the expected value if individuals were not influenced by the renovation of other group members plotted against the number of individuals involved (A) and the proportion of individuals involved (B). Plots are averages for each category and the line is the fitted line. Data where more than 7 individuals were involved were not included as occurring only in one group.

duration if individuals were acting independently. This was true for the absolute number of individuals as well as their relative number. More important, the renovation excess was linearly increasing with the number of individuals involved, as well as for the proportion of individuals involved.

The absence of specific signals associated with burrow renovation, together with the linear increase of number of individuals involved, recalls the classical concept of social facilitation (Zajonc, 1965; Clayton, 1978). Socially facilitated behaviours are defined as "an increase in the frequency or intensity of responses or the initiation of particular responses already in an animal's repertoire, when shown in the presence of others engaged in the same behaviour at the same time" (Clayton, 1978). It has also recently been shown that social facilitation can induce group vigilance in grey kangaroos *Macropus giganteus* (Pays et al., 2009).

The revealed absence of signalling could be due to three factors influencing the trade-offs of signalling. First, meerkats could be cognitively limited and unable to process such a signal. However, this is unlikely because meerkats are highly vocal and possess a wide range of signals, used in various contexts (Manser, 1998). Second, meerkats might not need such a signal to monitor the renovation behaviour of their group mates. This could be true, because the burrows are usually with little vegetation and without visual barriers between the group members. It would therefore be relatively easy to monitor another individual's renovation bout. Nevertheless, meerkats are often renovating alone. The most plausible explanation for this absence of signalling might be that coordination of renovation behaviour in meerkats is not extremely important. Indeed, meerkats did not renovate more (resp. less) when we artificially increased (resp. decreased) the amount of sand in their burrow (Christophe Bousquet, unpublished data). Furthermore, renovation probability and duration are not affected by whether or not meerkats return to the same sleeping burrow on the following night. Therefore, when renovating, meerkats appear not to maintain a clean burrow for the next night.

All together, meerkats do not need a signal associated with burrow renovation because (i) the risk to lose the group for each group member is low (renovation takes place while other individuals are in the same location) and (ii) the benefits derived from precise coordination among individuals are not high enough to justify the evolution of such a signal.

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CHAPTER 3

Moving Calls: a Vocal Mechanism Underlying Quorum Decisions in Cohesive Groups

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Moving Calls: a Vocal Mechanism Underlying Quorum Decisions in Cohesive Groups

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Summary

Members of social groups need to coordinate their behaviour when choosing between alternative activities. Consensus decisions enable group members to maintain group cohesion and one way to reach consensus is to rely on quorums. A quorum response is where the probability of an activity change sharply increases with the number of individuals supporting the new activity. Here, we investigated how meerkats (*Suricata suricatta*) use vocalizations in the context of movement decisions. Moving calls emitted by meerkats increased the speed of the group, with a sharp increase in the probability of changing foraging patch when the number of group members joining the chorus increased from two up to three. These calls had no apparent effect on the group's movement direction. When dominant individuals were involved in the chorus, the group's reaction was not stronger than when only subordinates called. Groups only increased speed in response to playbacks of moving calls from one individual when other group members emitted moving calls as well. The voting mechanism linked to a quorum probably allows meerkat groups to change foraging patches cohesively with increased speed. Such vocal coordination may reflect an aggregation rule linking individual assessment of foraging patch quality to group travel route.

Keywords: foraging patch; signal; vocalization; aggregation rule; quorum decision; meerkat

1. INTRODUCTION

Social species require decision-making processes in order to maintain their cohesiveness, allowing group members to benefit from advantages associated with group living. Signalling mechanisms that ensure group cohesion have been well studied in invertebrates and micro-organisms. Many of them rely on self-organization principles in which a pattern observed at the global level is the result of interactions among individuals "using only local information, without reference to the global pattern" (Camazine et al., 2001). For instance, individual amoebae of the slime mould *Dictyostelium discoideum* form multicellular slugs moving towards light. The cohesion of the slug during this phototaxis is mediated by a cascade of individual reactions to local changes induced by an external stimulus (the light, Marée et al., 1999). To maintain cohesion, some invertebrates use specific signals. For instance, individual army ants (*Eciton burchelli*) sigmoidally adjust their speed to the local concentration of a stimulus (the trail pheromone) produced by the ants themselves. The response to this signal allows army ants to display specific cohesion patterns under various environmental conditions (Franks et al., 1991). In other taxa, honeybees (*Apis mellifera*) form a swarm and move towards their new nest, when only a small proportion (approximately 5 %) of individuals know the final location. Nevertheless, the swarm remains cohesive because the informed scouts move faster than the naive bees, and naive bees are attracted by these fast streakers (Schultz et al., 2008). In vertebrates, empirical evidence shows that signals to maintain group cohesion are common in birds and mammals (Black, 1988; Boinski & Campbell, 1995; Prins, 1996; Byrne, 2000; Radford, 2004; Bourjade et al., 2009; Lusseau & Conradt, 2009; Ramseyer et al., 2009; Sueur & Petit, 2010). Yet the underlying mechanisms of these signals have not been thoroughly investigated.

Recently, cohesive collective movements have been considered as being the result of three different phases: the pre-departure, the departure itself and the post-departure (Petit & Bon, 2010). The use of signals usually characterizes the pre-departure period. The transition between the pre-departure and the departure onset often relies on "quorums" (Pratt et al., 2002; Conradt & Roper, 2005; Sumpter & Pratt, 2009). A quorum is the "minimum number of group members that need to take or favour a particular action for the whole group to adopt this action" (Conradt & Roper, 2005). As a consequence, "an individual's probability of selecting an option changes sharply when the number of like-minded conspecifics crosses a threshold"

(Sumpter & Pratt, 2009). It is therefore similar to the "quorum-sensing" mechanism described in microorganisms; for example, to synchronize the production of light by bioluminescent bacteria (Waters & Bassler, 2005). However, Redfield (2002) points out that quorum sensing in bacteria may in many cases be an artefact of "diffusion sensing" studied under laboratory conditions. In all cases, these quorum processes describe the accumulation of a specific signal to a certain threshold. Once this threshold is reached, the collective entity expresses a new behaviour or a new metabolic pathway.

Quorum decisions ensure that a minimum number of individuals (the actual quorum number) are ready to shift from one behaviour to the next. As decisions taken by several individuals are generally more accurate than decisions made alone (Kerr & Tindale, 2004; Codling et al., 2007), quorum thresholds reduce the risk of relying on only one individual and can minimize errors in decisions. Group decisions mediated by a quorum of individuals have been described in honeybees (Seeley & Visscher, 2003), ants (Pratt et al., 2002), fish (Ward et al., 2008) and humans (Vermeule, 2005). Yet the communicative or signalling mechanism underlying the quorum decision has only been quantified in insects (Pratt et al., 2002; Seeley & Visscher, 2003) and not in any vertebrate species besides humans (Vermeule, 2005).

Meerkats are cooperatively breeding mongooses, living across southern Africa in highly cohesive groups (a rare phenomenon in carnivores, Holekamp et al., 2000) varying from 3 to 50 individuals (Clutton-Brock et al., 2006). They forage together but do not share their food or hunt cooperatively; therefore, the benefits of group foraging behaviour are probably due to other benefits, such as reduced predation risk (Krause & Ruxton, 2002). Furthermore, while foraging for prey items living in the sand, meerkats often have their heads down or below ground, reducing the efficiency of visual communication (Manser, 1999). Potentially owing to this constraint, meerkats have evolved a wide range of vocalizations used in various contexts (Manser, 1998). Three types of spatial vocalizations in particular have been described in meerkats: the "close" call, the "lead" call and the "moving" call. The close call is emitted by all group members of a meerkat group throughout their foraging activity, and is the most frequently used call (Manser, 1998; Townsend et al., 2010). Its most likely function is to maintain each individual's space relative to other group members while searching for food. The lead call is emitted by an individual while moving fast in a straight line. Lead calls are mainly produced in the morning when meerkats leave

their sleeping burrow or after a predator alarm. Moving calls, on the other hand, are produced by meerkats while they are foraging. A meerkat starts to emit a moving call while foraging (i.e. before the individual has moved). Sometimes other foraging members join in what is called a "moving call chorus".

We investigated the mechanisms underlying group decisions in meerkats while foraging. We focused on the onset of changes of foraging patches when moving calls were emitted prior to any group movement. We investigated whether moving calls were associated with a change of location by the group, either by an increase in speed or by a change in travel direction. We then tested with playback experiments the effect of moving calls emitted by a single individual. Based on our observations of naturally occurring events when moving calls were emitted, we expected these playbacks to elicit group movement only when meerkats responded to them with moving calls.

2. MATERIALS AND METHODS

(a) *Study site and population*

We studied group coordination in meerkats at the Kalahari Meerkat Project, on ranchland in the South African Kalahari, near Van Zylsrus (26°58' S, 21°49' E). Data were collected during more than 100 group-hours, between August 2006 and November 2008. Description of habitat and climate are provided elsewhere (Clutton-Brock et al., 1999; Russell et al., 2002). All animals in the population could be individually identified by the use of unique dye mark combinations. Individuals were habituated to close observation (less than 1 m). The ages of almost all individuals (greater than 95 %) were known precisely (± 5 days), as well as most of their life-history events. We collected data on 12 habituated groups (group size varying from 6 to 19 individuals; mean group size: 10.8 ± 0.5), representing over 130 individuals. Owing to birth and death, group sizes of each focal group changed during the observation period, although within a small range.

(b) *Observation of moving calls*

We analysed 48 naturally occurring events of meerkats emitting moving calls from 12 groups (range: 1 – 12 events per group, average ± s. e.: 4 ± 0.95 events per group) that we followed during foraging over 2 – 3 h in the morning. Every 5 min

during these periods, we took GPS fixes of the location of the centre of the group (accuracy: 95 % of fixes within 5 m; eTrex H, Garmin International Inc., Olathe, KS, USA). In addition, when moving calls were emitted by either a single individual or several individuals, we recorded the location with an extra-GPS fix (Figure 1). Thus, the duration between the previous regular GPS fix and the extra "moving call GPS fix" could be any duration between 0 (moving call occurring during the regular GPS fix) and 4 min (moving call occurring 1 min before the next regular GPS fix).

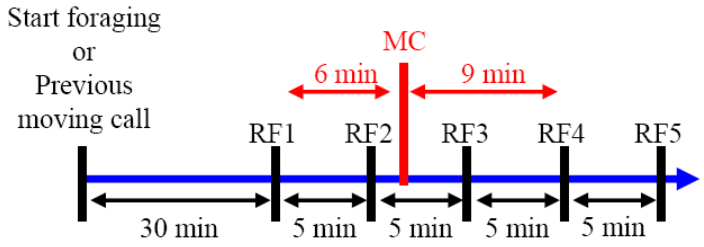

Figure 1. Overview of the protocol of GPS recordings. The thick blue arrow represents time. The first regular GPS fix (RF1) to be analysed was 30 min after the group started foraging or 30 min after the emission of a previous moving call event. Subsequent regular GPS fixes were continuously taken every 5 min (RF2 to RF5). A moving call's location was recorded by an extra-GPS fix (MC), which allowed the calculation of the average speed before the moving call (here from RF1 to MC) and of the average speed after the moving call (here from MC to RF4).

We decided to use the speed value over approximately 5 min to assess the immediate effects of moving calls. Further analysis showed that the results are qualitatively the same when we use approximately 10 or even 15 min (C. Bousquet 2010, unpublished data). To take into account the unpredictability of the moving call event, we calculated the average speeds in the following way: (i) "speed before the moving call": GPS point of moving call event (MC) in comparison to previous regular GPS fix (≥ 5 and < 10 min); and (ii) "speed after the moving call": GPS point MC in relation to the following regular GPS fix (≥ 5 and < 10 min; Figure 1). Only calling events occurring 30 min after the group started foraging or 30 min apart from each other (to ensure independence of events) were taken into account. For each moving call event, we recorded the number of callers involved (and their identity whenever

possible). We created four categories: one caller; two callers; three callers; and four or more callers. We did not further separate the latter category owing to difficulties in identifying all callers accurately when the group was spread over wide distances. For one group, we had no moving call chorus for the three-callers category. Thus, for statistical reasons, we had to merge the three-callers category with the four-or-more-callers category. The speed values for these two last categories were very similar. As a control for natural speed variations, we compared the speed 10 min before and 5 min before the calls occurred. As a further control, we assessed the group's speed difference owing to a naturally occurring close call by comparing the speed 5 min before a close call to the speed 5 min after that close call. Because of the high frequency of close call production, we always had close calls occurring at the same time (within a few seconds) as we took a regular GPS fix and therefore did not have to take an extra-GPS fix to coincide with close call emission.

Before and after moving call events, moving directions were measured from the previous regular GPS fix to the moving call GPS fix and from the moving call GPS fix to the next regular GPS fix, respectively. Afterwards, we calculated the angle of variation between the two moving directions.

(c) *Quorum number estimation*

Quorums are characterized by a sharp increase in the probability of exhibiting a behaviour, at a particular group size or quorum number. Such an increase can be mathematically approximated by fitting a sigmoidal logistic function to the observed data:

$$p_{SI} = \frac{\exp(-\beta T)}{\exp(-\beta T) + \exp(-\beta n)} \ , \qquad (1)$$

where p_{SI} is the probability of a speed increase and n is the number of callers. The parameter T defines the quorum number at which the probability of a speed increase is 0.5, while β determines the steepness of the response. The logistic function is convenient for fitting data since we can rearrange equation (1) to give

$$\log\left(\frac{p_{SI}}{1-p_{SI}}\right) = -\beta T + \beta n \, ,$$

allowing us to fit the relationship between p_{SI} and n using linear regression. For observations, we defined p_{SI} to be 1 if the change in speed was larger than that given

by the 95th percentile of speed changes in the control observations; otherwise p_{SI} was zero. The procedure was run in MATLAB 7.7.0 (The MathWorks, Inc.).

(d) ***Playbacks of moving calls***

To test whether the moving calls were the causal factor to initiate group movement, we performed playback experiments. We recorded moving and close calls of the group's dominant female by following her within 1 – 2 m with a Sennheiser ME66 directional microphone (Sennheiser Electronic Corp., Old Lyme, CT, USA), with windshield, connected to a solid-state recorder (Marantz PMD660, D & M Professional, Kanagawa, Japan; sampling frequency of 44.1 kHz). We edited the calls using COOL EDIT 2000 (Syntrillium Software Corporation, Phoenix, AZ, USA). An edited sound file to be played back consisted of three different moving calls (test condition) or three different close calls (control condition), each separated by 2 s of silence (similar structure to a naturally occurring moving call bout), with an overall duration of 8 s.

Playbacks were conducted with the Marantz recorder connected to a portable loudspeaker (Hama AS-61 10W, Hama GmbH & Co KG, Monheim, Germany) at an amplitude similar to that in the wild (estimated by hearing). The loudspeaker was attached to the leg of the observer at the height of a foraging meerkat. All playbacks were made in the centre of the group, with no meerkats present within 5 m of the loudspeaker when the playback started (most of the group members were 5 – 10 m away from the loudspeaker). We video recorded (Everio GZ-MG150 digital video camera, JVC, Yokohama, Japan) the maximum visible number of meerkats to assess their first reaction. At the time of playback, all individuals were foraging and no sentinel had been on duty for at least 10 min. No natural moving calls had occurred in the previous 30 min. We took a GPS fix of the playback's location. If a disturbance (alarm call, intergroup encounter, presence of a car or another human) occurred within 5 min after the playback, the experiment was discarded (which was the case for two playbacks). We conducted moving call playbacks in six different meerkat groups until we had for each group at least one "vocal response" and one "no vocal response". Therefore, depending on groups, we conducted two or three playbacks. As a control, we played back close calls in five different groups. We ran two playbacks in each group, except for one group in which only one close call playback was possible owing to time constraints. We then compared the speed 5 min before the playback to the

speed 5 min after the playback. Angles for movement direction changes were determined as described before. To avoid habituation, we waited at least 7 days between any two consecutive playbacks for a focal group.

(e) ***Statistical analysis***

Statistical tests were done using SPSS 16.0 for Windows (SPSS Inc., Chicago, IL, USA). We compared meerkat group speed by using paired exact Wilcoxon signed-ranks tests, where the speed after the considered call was linked to the speed before the call. To test the influence of the number of callers, we conducted Friedman tests. For the test of dominance and number of callers, we used the Scheirer–Ray–Hare test, which is a non-parametric equivalent of a two-way ANOVA (Dytham, 2003). We conducted Watson–Williams tests to compare mean angles (Zar, 1999). For the analysis of the playback experiments, we calculated the average speed per group for the playback experiments within the same condition—such as: (i) test condition, moving calls with "no vocal response" (n = 6); (ii) moving calls with "vocal response" (n = 6); and (iii) control condition, close calls (n = 5), and performed exact Wilcoxon signed-ranks tests.

3. RESULTS

(a) ***Moving calls increase speed***

When meerkats emitted moving calls, the group's speed increased, but not when they emitted close calls. The group's speed in the 5 min before the naturally occurring moving calls was 3.31 ± 0.33 (mean ± s. e.) $m.min^{-1}$. The group's speed in the 5 min after the naturally occurring moving calls was 7.06 ± 0.85 $m.min^{-1}$ (exact Wilcoxon signed-ranks test: Z = -3.059, N = 12, $p < 0.001$). Therefore, meerkat groups travelled twice as fast after a moving call event versus before. By contrast, naturally occurring close calls did not affect group speed (average speed in the 5 min before a close call: 3.33 ± 0.52 $m.min^{-1}$; after a close call: 3.09 ± 0.35 $m.min^{-1}$; exact Wilcoxon signed-ranks test: Z = -0.524, N = 5, p = 0.69). When taking the social status of the callers into consideration, we found no effect of dominance on the movement of the group. Events with moving calls in which dominant individuals were involved did not affect the group speed more than moving call events in which only subordinate individuals were involved (Figure 2 and Table 1).

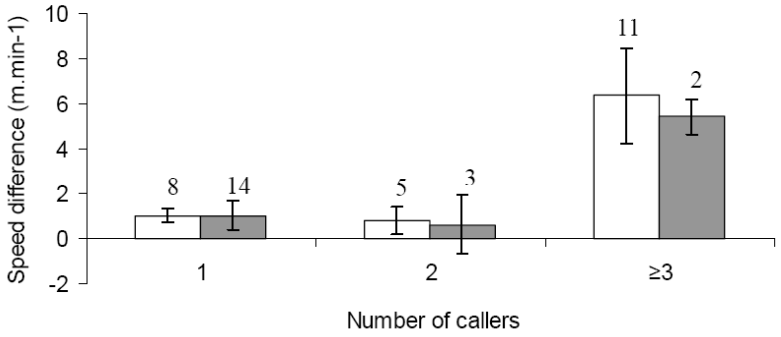

Figure 2. Effect of social status on the speed difference from before emitting moving calls to the period afterwards. White bars indicate events involving at least one dominant individual calling, grey bars when only subordinate individuals called. Numbers above bars indicate the number of events for each category. Mean ± s. e.

Table 1. Scheirer–Ray–Hare test output. SS, sum of square; d.f., degrees of freedom; MS_{tot}, mean sum of square of the total; SS/MS_{tot}, ratio sum of square of the factor by the mean sum of square of the total.

	SS	df	MS_{tot}	SS/MS_{tot}	p
Dominance	0.5	1		0.011	0.918
Nb callers	580.0	2		12.608	0.002
Interaction	6.5	2		0.142	0.932
Total	1012.0	22	46		

(b) ***Quorum of two or three individuals necessary to increase group speed***

Moving calls dramatically affected the group speed when three or more callers joined the chorus (Figure 2; Friedman test: $\chi^2 = 9.333$, N = 6, d. f. = 2, $p = 0.006$). When taken on their own the categories, "one caller" and "two callers" showed a small and non-significant increase in speed (one caller: $+0.79 \pm 0.61$ m.min^{-1}, exact Wilcoxon signed-ranks test: $Z = -1.363$, N = 6, $p = 0.22$; two callers: $+1.55 \pm 0.64$ m.min^{-1}, exact Wilcoxon signed-ranks test: $Z = -1.782$, N = 6, $p = 0.09$). However, when three or more callers were involved in the chorus, the group speed increased much more ($+6.54 \pm 1.82$ m.min^{-1}, exact Wilcoxon signed-ranks test: $Z = -2.201$, N = 6, $p = 0.03$).

The importance of three calling individuals in increasing group speed is further clarified when the logistic function (equation (1)) is fitted to the probability of

increasing speed. In the control observations, 95 % of changes in speed were less than 2.69 m.min^{-1} (dotted line in Figure 3A). Figure 3B shows the proportion of observations in which increase in speed was greater than 2.69 m.min^{-1}. Fitting to these observations gives an estimate of the quorum number of $T = 2.57$, suggesting that the switch from two to three callers marks the point at which a speed increase is highly probable. When only close calls were emitted, the group's speed increase never reached 2.69 m.min^{-1}.

(c) Vocal response required for playbacks to increase group speed

The vocal response to the playbacks of moving calls from the dominant female also had an impact on the increase in group speed (vocal response: +2.78 ± 0.82 m.min^{-1}, exact Wilcoxon signed-ranks test: $Z = -2.201$, N = 6, $p = 0.028$; Figure 4). In contrast, playbacks of moving calls that did not elicit a vocal response did not affect group speed (no vocal response: -0.65 ± 0.39 m.min^{-1}, exact Wilcoxon signed-ranks test: $Z = -1.483$, N= 6, $p = 0.138$; Figure 4). Close calls of the dominant female played back to the foraging group (N = 9 in five groups) did not influence the group speed (+0.38 ± 0.67 m.min^{-1}, exact Wilcoxon signed-ranks test: $Z = -0.677$, N = 5, $p = 0.5$).

(d) *Moving calls do not influence travelling direction*

Meerkats did not change their moving direction more after moving calls than after close calls. When meerkats emitted moving calls, the group's direction for the next 5 min changed by 49.1 ± 26.7° (mean angle ± angular deviation; N = 12) from the straight line (either on the left or on the right). The number of callers involved in the moving call chorus did not affect this turning angle. The change of direction after a moving call did not differ from the one following a close call (Watson–Williams test: $F = 0.07$, $p > 0.25$), which was 43.9 ± 46.1° (N = 6) from the straight line (either on the left or on the right). Playbacks of moving calls did not affect the direction change of the group when compared with playbacks of close calls (62.7 ± 32.3°, N = 6 and 70.2 ± 21.0°, N = 5, respectively; Watson–Williams test: $F = 0.16$, $p > 0.25$). Playbacks themselves did not have an effect on the group's direction as direction changes after playbacks did not differ from the direction changes after naturally occurring calls (61.7 ± 24.1°, N = 6 and 54.0 ± 30.6°, N = 12, respectively; Watson–Williams test: $F = 0.25$, $p > 0.25$).

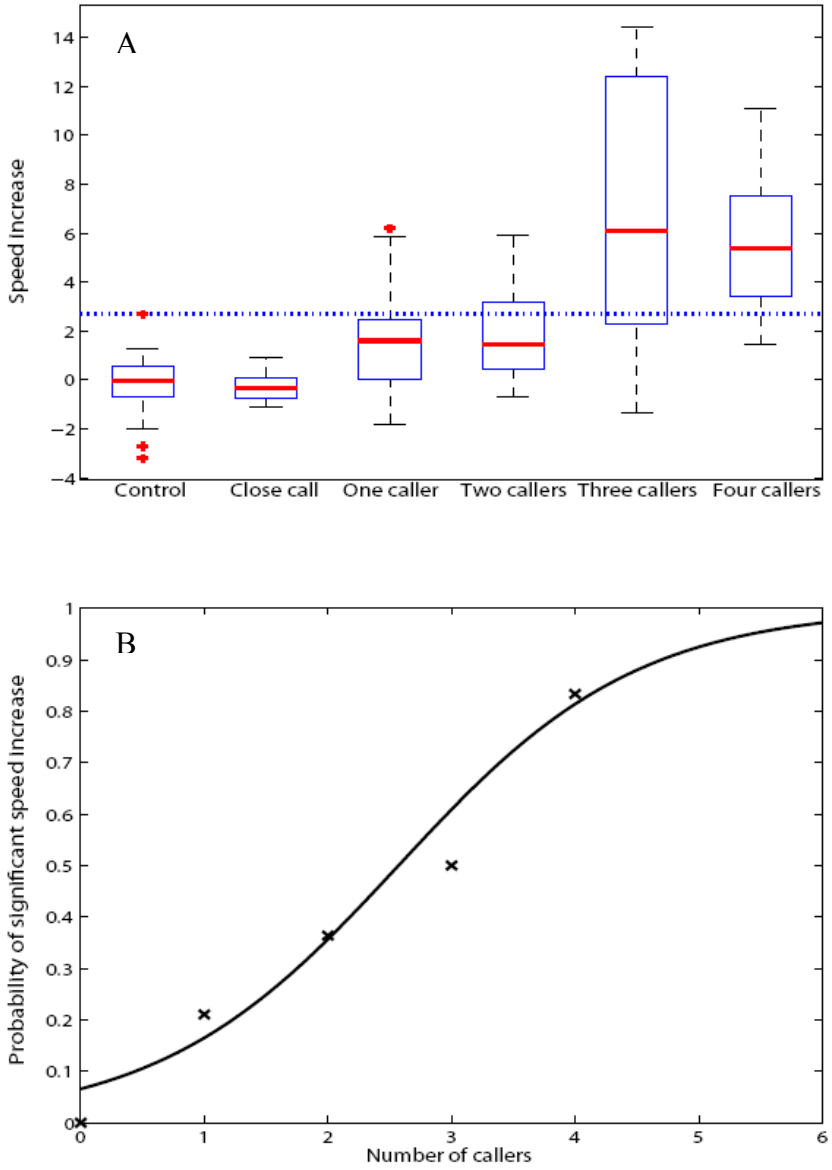

Figure 3. A) Effect of the number of callers involved in the moving call chorus on group speed increase. The box plots give distribution of speed increases (minimum, first quartile, median, third quartile, maximum; asterisks represent outliers). The dotted line at 2.69 m.min^{-1} indicates the 95 percentile of the distribution of speed changes in the control observations. B) Identification of the quorum number required for an increase in speed. Crosses represent the proportion of moving calls inducing a speed increase higher than 2.69 m.min^{-1}. The dark line represents the fit of the sigmoidal logistic function (equation (1)) to the data. Parameter values determined by logistic regression are $T = 2.57$ and $\beta = 1.03$.

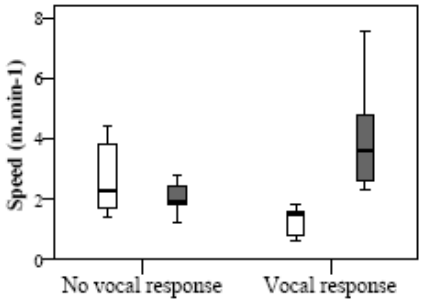

Figure 4. Effect of the presence or absence of a vocal response to the playback of moving calls on group speed. White bars, speed before a playback; grey bars, speed after a playback. For the box-plots, the bottom and top of the box represent the first and the third quartiles, respectively, and the line inside the box shows the median. Limits of the whiskers represent minimum and maximum values of the data.

4. DISCUSSION

Meerkat groups remained cohesive during daily foraging, with groups only splitting up owing to external events such as predator approaches. Part of their group movements were initiated by specific vocalizations, the moving calls. Our results from natural observations, a mathematical model and playback experiments suggest that a quorum of at least two and usually three meerkats emitting moving calls are necessary for the whole group to move to a new foraging patch. If no other group member or only one joined the moving call chorus to support the initiator's motivation, then the group and the initiator usually continued to forage in the same patch. The initiator's signal became effective if at least two other meerkats supported its preference. In both cases, the group remained cohesive despite conflicting interests (or at least conflicting information) among group members. This cohesion is crucial for meerkats' survival, as single individuals outside their group have a higher mortality rate (Clutton-Brock et al., 1999). Our results therefore suggest that meerkats use a specific vocalization (the moving call) along with a quorum response mechanism as an efficient temporal coordination tool of group movement.

The effect of moving calls on group direction did not differ from the effect of close calls on group direction. This indicates that moving calls are not used as a directional coordination tool. Given that meerkats' prey are widely distributed and underground, it might be more relevant for meerkats to know *when* it is best for them to leave the current foraging patch rather than *where* to go next. However, once the

quorum is reached in the group, some individuals might still choose the next direction. A closer look at the position of specific individuals (e.g. dominant pair, older individuals) might reveal that the choice of the next direction is not random.

Overall, the use of moving calls may function as a foraging-patch quality census system. A meerkat might emit a moving call when its immediate foraging patch is becoming food-depleted. If other meerkats, at a similar time, also find their foraging patch poor, then they might join the chorus. That a quorum of callers has been reached reflects an accumulation of evidence that a foraging patch is depleting. Such a system avoids errors where one unsuccessful individual wrongly concludes that food is depleted. In order for its call to be followed as a signal to leave, at least one and usually two other individuals have to emit similar calls. The fact that neither dominance status, sex nor age (disregarding pups and juveniles) of callers affected the success of moving calls further supports the idea of move calling as reflecting each individual's assessment of food patch quality. Such a quality census system on foraging patches fits well many of the observations described in primates (Boinski, 2000; Petit et al., 2009) and birds (Ramseyer et al., 2009), as well as theoretical models (Cant & Shen, 2006; Rands et al., 2003; Rands et al., 2008; Valone, 1993). Thus, it provides a simple mechanism to coordinate group cohesion effectively with maximized foraging success for the majority of the group.

Moving calls are emitted *before* meerkats increase their speed, and are not just a by-product vocalization emitted by meerkats on the move. They act as a signal *prior to* group movement. This signal can still be used during group movement, potentially to reinforce its meaning. In quorum decisions, the signal eliciting the new behaviour does not necessarily have to stop being produced once the threshold is reached. For example, in quorum-sensing bacteria, the signal is even reinforced by the newly released metabolic pathway (figure 1 in Waters & Bassler, 2005). Additionally, in vertebrates, quorum thresholds have been described for which the signal used was the mere movement of individuals, without any vocalizations (Ward et al., 2008; Sueur et al., 2010). In this case, the signal used (the displacement itself) does not disappear once the threshold is reached as the group continues to move.

Another intriguing aspect of our findings is the absolute value of the quorum number: two to three individuals. Other studies in the field (Bourjade et al., 2009; Sueur & Petit, 2008; Sumpter et al., 2008) also found similar results. For example, it takes more than two fish to make a decision in groups ranging up to 10 individuals

(Sumpter et al., 2008). In macaques, for two groups of 22 individuals, approximately three individuals were involved in pre-departure behaviour, which was linked to the departure success (Sueur & Petit, 2008). In horses, approximately three horses in a group of six individuals were involved, on average, in pre-departure behaviour (Bourjade et al., 2009). It appears that two to three individuals acting as signallers is a common requirement in several species, at least for group sizes ranging from 6 to 22 individuals. Increasing the quorum number as group size increases could potentially increase the frequency of group splits, owing to the "strength in number" effect (Dyer et al., 2009). However, there may also be a cognitive limitation in distinguishing among more than three individuals. Indeed, a quorum number does not need to be large to be effective since errors decrease exponentially with quorum size. If the probability that one meerkat wrongly concludes that it is time to leave a foraging patch is ε = 5 per cent, then the probability that two and three individuals will independently reach the same conclusion is $\varepsilon^2 = 0.25$ per cent and $\varepsilon^3 = 0.0125$ per cent, respectively (Sumpter, 2010).

The mechanism underlying the changing of foraging patches initiated by a single individual, but only successful with the support of additional group members, probably represents a common group coordination process in many vertebrate species (primates: Petit et al., 2009; fish: Ward et al., 2008), including humans (Faria et al., 2010). This study, however, is a first step with wild animals towards understanding how individual decisions and group decisions are linked, and how a group's behaviour can result from the aggregation of individual behaviours, following a specific aggregation rule (Conradt & List, 2009). The aggregation rule of using calls allows a fast change in behaviour or direction, without relying on only one or two individual assessments. In essence, it reflects a so-called voting process (Prins, 1996; Sellers et al., 2007), where the preference of several group members is expressed, and only then, depending on the support of enough individuals to reach the quorum needed, does the according alternative action follow. Previous studies have shown the importance of vocalizations in vertebrates to change foraging patches (Radford, 2004). Here, we showed that the response of group members to the initiator's call determined the final group's response. This effect can be termed as "social feedback", where followers responding to an initiator are important for the success or the failure of the initiator (Harcourt et al., 2009; Petit & Bon, 2010; Petit et al., 2009). These

approaches provide important insights into better understanding the transition from individual behaviour to group behaviour.

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CHAPTER 4

Factors Influencing Spatial Positioning in Cohesively Foraging Groups

To be submitted

Factors Influencing Spatial Positioning in Cohesively Foraging Groups

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To be submitted

Summary

Spatial positioning within groups is thought to be of broad importance for each individual to maximise the benefit-to-cost ratio of its own location. This ratio may be affected by individual constraints, such as age, condition influencing foraging skills or social constraints due to attraction or avoidance of other group members. The knowledge of the geometry of a group enables to conduct social network analysis to assess the social relationships within the group, which can become more accurate when precise positions and associated behaviours are recorded. Such a precision can be reached by the use of GPS devices with simultaneous observations of behaviours of the individuals. We studied spatial positioning in meerkats (*Suricata suricatta*) which live in cohesive groups. Our data show that dominant individuals are more frequently in the front of their foraging group than expected by chance. We also found that individuals exhibiting preferential associations were more frequent than predicted by random networks. Additionally, we detected no difference of individual trajectories within the dominant pair. Finally, our study reveals the advantages that can be derived from applying precise GPS recordings to each individual. Incorporating spatial data into ecological and behavioural studies will provide an opportunity to control for variables so far rarely controlled for, like inter-individual distances.

Keywords: spatial position; GPS-recordings; meerkats; foraging route; social network

1. INTRODUCTION

Different spatial positions within a group have differential costs and benefits (Krause, 1994). Individuals in the centre of their group face less predation costs (Hamilton, 1971), while individuals in the periphery have earlier access to foraging resources (Robinson, 1981). The geometry of a social group enables to determine which individuals are close to each other and which ones are further away from each other. However, the metric positioning of individuals might not be the only measure of interest, as sometimes topological positioning (i.e., the actual number of neighbours is more important than their distance) can be seen to have a major impact on animal aggregations (Ballerini et al., 2008). Individuals also vary in their reaction to the spatial positioning of other group members. For instance, shy individuals move more often towards each other than bold individuals (Sibbald et al., 2009) and close relatives can be closer to each other than lesser-related individuals (Nituch et al., 2008). Furthermore, the spatial shape of a group and its underlying coordination mechanisms are also important to determine the future spatial organisation of the same group (i.e., the group has a "collective memory", Couzin et al., 2002) and can shed some light on how animal groups change from one collective state to another.

Recently, the study of spatial group structure has received considerable attention, due to the fast development of computing techniques in social network analysis (Lusseau, 2003; Wey et al., 2008; Whitehead, 2008; Gygax et al., 2009; Krause et al., 2009). Furthermore, with decreasing sizes of portable GPS devices, the measurement of spatial positions is getting so precise that the influence of spatial positioning can be more routinely integrated into ecological and behavioural studies (Biro et al., 2006; Gygax et al., 2009; Nagy et al., 2010; Šárová et al., 2010). However, these studies mainly deal with domesticated species retained in relatively small enclosures and without environmental challenges. Due to their capacities, such studies on animals in their natural habitat would allow to incorporate environmental factors in the analysis, as shown in a study on homing pigeons (*Columba liva*) (Nagy et al., 2010). In this study, researchers formed groups of up to 10 domesticated pigeons and analysed via GPS devices the homing route of the group and of each individual pigeon. They found a strong correlation between an individual's average position and its place in the dominance hierarchy (Nagy et al., 2010). This phenomenon has also been found in beef cows (*Bos taurus*) and has been termed "graded leadership" (Šárová et al., 2010). Overall, precise positioning knowledge can

help to estimate more accurately inter-individual distances. Because several interactions are not possible anymore once inter-individual distances are bigger than a specific threshold, knowledge about these distances will help to determine the actual available time for a particular interaction type (which is not necessarily the whole observation period as often assumed, Figure 1).

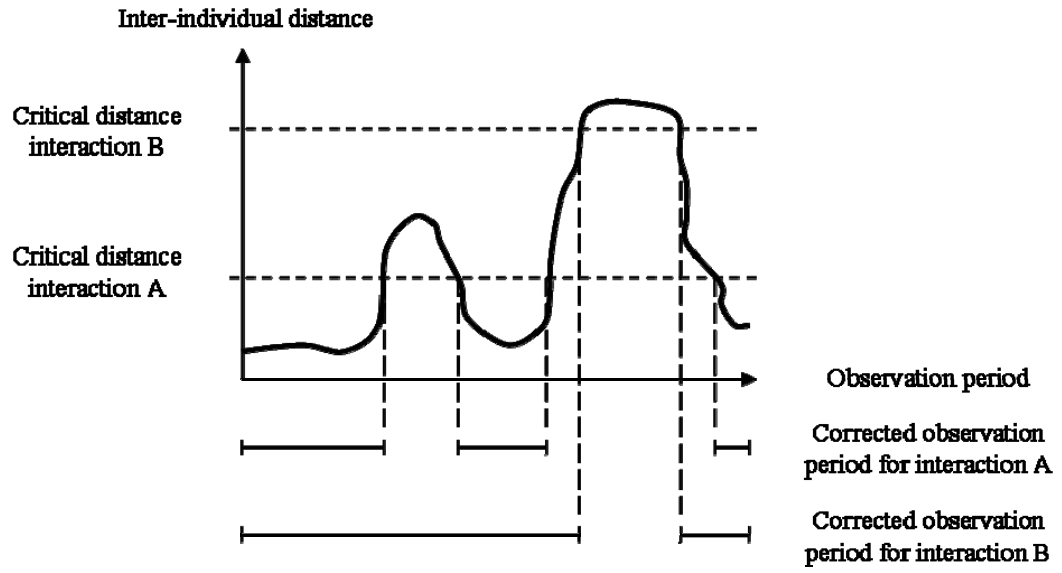

Figure 1. Effect of inter-individual distance on observation time. Distance between two individuals varies through time. Certain interaction types (A or B) are only possible when the individuals are below a critical distance from each other. Knowing the inter-individual distances therefore allows assessing more precisely the actual observation period for each interaction type.

Meerkats live in the southern Kalahari and form cohesive social groups. They forage together but do not share food among adults and foraging competitions occur frequently (Barnard, 2000). Groups are formed of individuals from both sexes and of various ages (van Staaden, 1994) and one individual of each sex retain social dominance and monopolize reproduction (Clutton-Brock et al., 1999b; Hodge et al., 2008). Therefore, meerkat groups are of heterogeneous composition related to sex, age, dominance status and condition. Meerkats also have large territories relative to their body size which they fiercely defend against intruders (Jordan et al., 2007). Furthermore, meerkats are under high predation pressure (Clutton-Brock et al., 1999a)

and foraging success correlates strongly with reproductive success (Hodge et al., 2008). Therefore, individuals able to choose an optimal spatial positioning could have an advantage in breeding competition.

In this study, we assess the importance of spatial positioning for meerkats within their group by conducting several observations with different methods. With scan data on spatial locations (Altmann, 1974), we determine which individuals are in the front of the foraging group. With the help of social network analysis (Whitehead, 2008), we investigate the formation of sub-groups during foraging and the existence of potential avoidance/attraction effects. Finally, with the help of accurate GPS data (Gurarie et al., 2009), we evaluate whether the dominant female and the dominant male differ in their individual trajectories. All together, these data provide an insight on how precise knowledge of spatial relationship among group members can help to understand better the organisation of a group and how this organisation develops over time.

2. MATERIAL AND METHODS

(a) *Study site and population*

We studied the influence of spatial positioning within a group in meerkats on the wild but habituated population of the Kalahari Meerkat Project, on ranchland in the South African Kalahari, near Van Zylsrus (26° 58' S, 21° 49' E). Data were collected during more than 100 group-hours of observations, between August 2006 and November 2008. Description of habitat and climate are provided elsewhere (Clutton-Brock et al., 1999b; Russell et al., 2002). All animals in the population could be individually identified by the use of unique dye mark combinations. Individuals were habituated to close observation (< 1 m). The ages of almost all individuals were known precisely (± 5 days) as well as most of their life-history events (except on immigrants, < 5 % of the individuals).

(b) *Spatial positions within the group*

We conducted scan-sampling of individual positions within 9 meerkat groups from August to November 2006, with additional data in August 2008. Every five minutes once the group started foraging, we recorded the identity of the first individual in the front of the group. The overall direction of travel was assessed

between two scans by the straight line between the locations of the group centre during these two scans. We included only sessions with more than 5 scans (range: 5 to 22 scans per session). The shape of a foraging meerkat group is similar to a moving amoeba and it is not always easy to locate the front of the group (C. Bousquet, pers. obs.). However, once in the group, this task becomes easier, in particular when remembering the previous route of the group (C. Bousquet, pers. obs.). The observed value is the number of time an individual was seen at the front of the group. The expected value is the reciprocal of the group size multiplied by the number of scans during a focal session. Therefore, the observed-to-expected ratio indicates whether an individual was more or less often than expected in the front of the group. A ratio value of 2 means that an individual is observed twice as often as expected in front of its group while a value of 0.5 means that the individual is observed half often as expected. For the study of sex and social status, we restricted our analysis to adults of more than 2 years because this was the only age category likely to be in the front of the group (see Results on influence of age).

(c) *Sub-group composition*

Data on sub-group composition were collected on the same 9 meerkat groups as in 2.(b) from August 2006 to March 2007, from July 2007 to October 2007 and from June 2008 to August 2008. Group sizes varied from 6 to 17 adults. Despite foraging cohesively as a group, meerkats can be more or less spatially close (range: a few centimetres to 20 m) to other group members. We documented sub-group compositions every time we saw meerkat sub-groups more than 10 m away from any other sub-groups. We opted for this threshold because over this limit, meerkats tend to come closer together (pers. obs.). Sub-groups could consist of only 1 individual if this individual was more than 10 m apart from the rest of the group. Additionally, we also recorded which individual was moving from one sub-group to another and in which sequence this was done. All movements were documented until the group was united again (i.e., less than 10 m between each group member). When sub-groups were fusing again due to small foraging movements, we defined the re-union of the group as due to foraging.

Once sub-groups were formed, the whole group reunited (i.e. every group member were within 10 m of another one) on average 286 ± 18 s later. To minimize pseudo-replication, we restricted our analysis to sub-group compositions which were

separated by more than 15 minutes from each other. The retained 532 sub-group compositions (range: 18 – 118 per group) were entered in the software SOCPROG 2.4 (Whitehead, 2009b) to conduct a social network analysis on 9 focal groups. For each group, we determined several social network parameters. First, we assessed the level of social differentiation in each group (Whitehead, 2008). Values less than 0.3 indicate homogeneous societies while values greater than 0.5 indicate well differentiated societies. However, these values are only useful if the correlation coefficient between true and calculated association indices is close to 1. We therefore present the correlation coefficients to determine the power of the analysis to detect the true social system (Whitehead, 2008). Second, we assessed whether specific individuals within a group consistently avoided (resp. preferred) each other by considering whether their association index was low (resp. high) enough by running simulations with 40,000 permutations and 10 trials per permutations (Bejder et al., 1998; Whitehead, 2008). Finally, these simulations also allowed us to assess whether each individual was more probably present in a small or a large sub-group by comparing each individual's typical group size (Whitehead, 2008). Presence of individuals in large or small groups could reflect the social preference of the individual and/or its personality (Michelena et al., 2009).

(d) ***Individual trajectories***

We equipped the dominant pair of 7 meerkat groups with GPS collars (GiPSy, TechnoSmart s. r. l., Rome, Italy). We focused on the dominant pair because we did not have enough devices to equip all adults within a group. Furthermore, the two dominant individuals are the less likely individuals to leave their group (Young et al., 2007), increasing the chances to collect comparable data. Each equipped animal was captured and anaesthetised to enable the fitting of a temporary collar around its neck (Jordan et al., 2007). The collar was fitted with a Velcro strip which allowed to attach and to detach the GiPSy GPS device. The collar and the GPS device were weighing altogether less than 20 g. At the end of the recording period (range: 3 to 9 hours of recordings), the GPS device was removed from the individual. To assess the relative positioning of the 2 individuals, we synchronised the GPS together, by using two settings for the GPS recordings. In the first one, the GPS were on 37 seconds per minute and the first 6 seconds of the recordings were discarded (to allow good accuracy of the signal). Once we downloaded the data, we calculated the average

location for the 31 remaining seconds. In the second setting, we recorded data continuously on both GPS. After performing the first setting in 2 groups, we switched to the second one for the 5 remaining groups because we realised we had enough battery to leave the GPS on for the approximately 3 hours of data collection. For the 5 last groups, we also stopped attaching the GPS device directly to the animal, as the risk of losing the device was too high. Then, the two individuals were followed by two observers on foot who followed precisely their focal meerkat's track. Once the recording procedure was over, data were downloaded on a PC computer. We then averaged data for each minute of recordings to compare the dominant individuals' positions every minute. In particular, we assessed the distance travelled by each individual and which individual was in front of the other. For the last measurement, we took the smoothed average trajectory as a reference. Furthermore, an individual was either considered as being "static" (when the distance travelled between two consecutive minutes was smaller than the average distance for that individual, representing foraging behaviour) or "dynamic" (when the distance travelled between two consecutive minutes was bigger than the average distance for that individual, representing moving individuals). Analyses presented here focus on periods during which both individuals were classified as "dynamic", to avoid the influence of foraging on individual trajectory.

(e) ***Statistical analysis***

For the analysis of scans, we conducted generalised mixed-effect models in R 2.10.0 (R development core team, 2009) for each of the relevant category (age, sex or social status). We used the quasipoisson distribution and we fitted individual nested within group as a random term. To avoid confounding factors, we ran the model for age on a data subset without dominant individuals, which are also the oldest in a group. Similarly, we ran the model for dominance on a data subset with only adults of similar age as the dominants in the group (within one year of the youngest dominant individual). Each model was then tested with an ANOVA against the null model containing only the intercept as a fixed effect and the same random effect. The result of that ANOVA gave the significance level for the relevant category (age, sex or social status). To assess the difference of trajectory length between the dominant male and the dominant female (which was modelled with a quasipoisson distribution), we run a generalised mixed-effect model with sex as the explanatory variable and group

as a random term. To assess whether a dominant individual was more often in front of the other one (which was modelled with a quasibinomial distribution), we run a generalised mixed-effect model with sex as the explanatory variable and group as a random term. For the sub-group composition, we compared the observed values to the expected values from the simulations by performing exact Wilcoxon signed ranks tests in SPSS 16.0 for Windows (SPSS Inc., Chicago, USA).

3. RESULTS

(a) *Spatial positions within a group*

The spatial position of an individual depended on age and dominance status, but not on sex. Adults more than 2 years-old were more likely to be in the front of their group than any other age category (generalised mixed-effect model: $\chi^2 = 9.04$, d. f. = 3, $p < 0.05$, Figure 2A). Dominant individuals were also more often in the front of the group than subordinates (generalised mixed-effect model: $\chi^2 = 15.45$, d. f. = 1, $p < 0.001$, Figure 2B). Females and males did not differ in their propensity to be in the front of the group (generalised mixed-effect model: $\chi^2 = 0.41$, d. f. = 1, $p > 0.5$, Figure 2C).

(b) *Sub-groups*

Group size did not affect the number of sub-groups formed during foraging (Pearson correlation r = 0.08). The average social differentiation for the 9 focal meerkat groups was 0.316 ± 0.052 (range: 0.107 - 0.545), suggesting that meerkat groups are rather homogeneous while foraging (Whitehead, 2009a). However, two groups (Drie Doring and Gattaca) showed values greater than 0.5 (0.501 and 0.545, respectively), indicating differentiated social structure (Whitehead, 2009a). For these two groups, the correlation coefficient between true and calculated association indices was maximal (1.000). Overall, correlation coefficients were very high (0.844 ± 0.041, range: 0.678 -1.000) indicating that our samples allowed to detect the true social system (Whitehead, 2009a). The permutation tests revealed that, for all groups except one (Zappa), more meerkats exhibited preferential associations (avoidance or attraction) than expected by chance (observed: 8.22 ± 1.57 individuals; expected: 3.39 ± 0.67 individuals; exact Wilcoxon signed ranks test, N = 13, $Z = -2.429$, $p < 0.05$). Furthermore, for all groups except one (Zappa), more meerkats were in sub-

groups of unusual typical group size (small or large) than expected by chance (observed: 2.56 ± 0.41 individuals; expected: 0.58 ± 0.06 individuals; exact Wilcoxon signed ranks test, N = 13, Z = -2.547, $p < 0.01$).

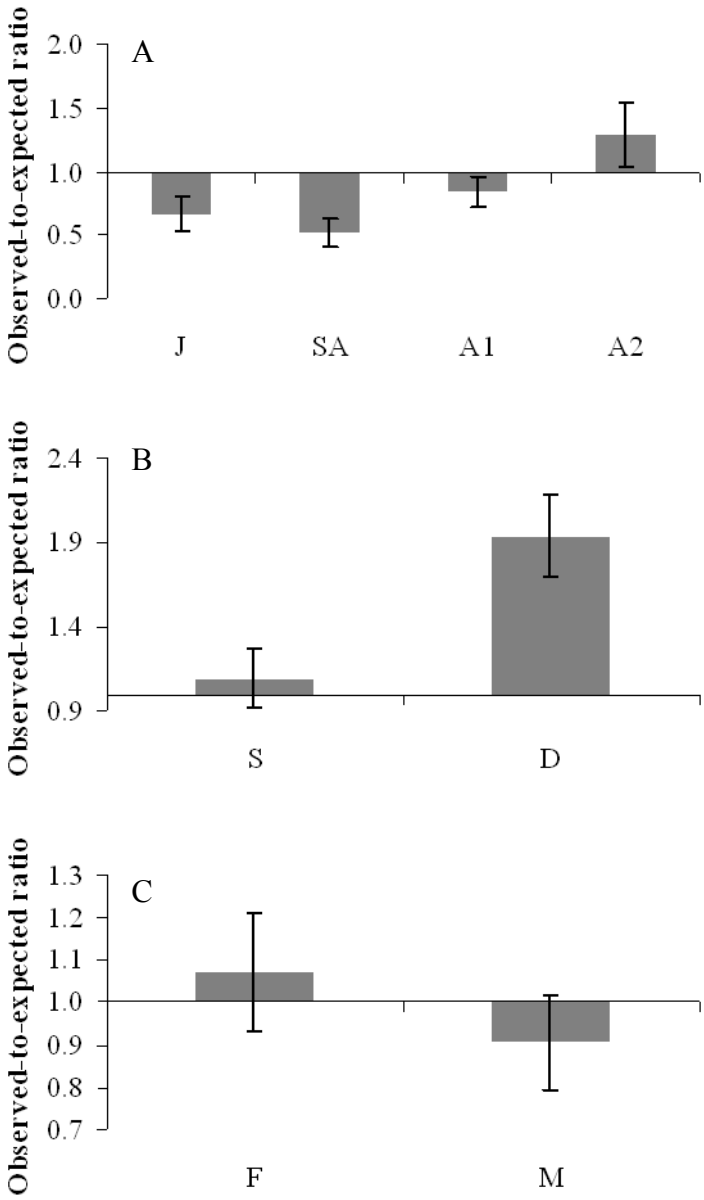

Figure 2. Effect of social categories on the observed-to-expected ratio of being in front of a foraging group. A) Age category (dominant individuals removed from analysis): J: Juvenile, SA: Sub-adult, A1: Adult 1, A2: Adult 2. B) Dominance status (only adults at most 1 year younger than the youngest dominant): S: Subordinate, D: Dominant. C) Sex (only adults included): F: Female, M: Male. Mean ± se.

(c) *Individual trajectories*

In the 7 groups where we investigated continuously the movement of the dominant pair, the female (15.15 ± 1.12 m.min^{-1}) covered the same distance per minute as the male (14.83 ± 0.41 m.min^{-1}, generalised mixed effect model, with group as a random term: $\chi^2 = 0.108$, $p > 0.7$). Furthermore, none of the two dominant individuals was more often in front of the other (female: 50.10 ± 1.72 %, male: 49.90 ± 1.72 %, generalised mixed effect model, with group as a random term: $\chi^2 = 0.020$, $p > 0.8$).

4. DISCUSSION

Dominant meerkats were found more often than expected in the front of foraging groups. Despite being cohesive in their daily routes, meerkat groups sometimes temporarily formed sub-groups and some individuals were consistently found in small or large sub-groups. Furthermore, some individuals avoided each other and others attracted each other more often than expected by chance. Finally, the dominant female and the dominant male did not differ in the length of their foraging route, nor in who was in the front of each other.

In another study on the same population with a different methodology, Barnard (2000) also found that the dominant pair occupies front positions. With our study, we additionally controlled for expected values of being in the front, which did not affect the results. Dominants therefore increased their foraging benefits, as individuals in the front spend more time foraging (Barnard, 2000). The benefit might be greater also if subordinates were spatially avoiding dominants. Despite cases of clear avoidance between individuals, this does not seem to be the systematic case. Indeed, it was not possible to assess any particular category of individuals showing preferential associations or avoidances towards other categories of individuals. With our available dataset, we did not detect that females avoid females or that subordinates avoid dominants, for example. However, this might be a limitation of our current data and more work in this direction should be rewarding. There is more variation in the association indices calculated in our study than expected by chance and by measuring sub-group composition more systematically and more accurately, one should be able in the future to disentangle the causes of this high variation (Whitehead, 2008).

Our results from GPS devices showed that new techniques of data acquisition on spatial positioning can be transposed to meerkats. Our data on individual trajectories and their influence on group trajectory did not show any difference between the dominant male and female. It therefore seems like the influence of these two individuals on the group trajectory is identical. It would be highly rewarding to increase the number of individual equipped and the number of days of recordings. One way to reach this promising research would be to displace the GPS devices from the meerkats to mobile antennas carried by field observers. Then, the relative positioning of each meerkat could be obtained by equipping all adults of a chip readable by each antenna. As the chip is much lighter and necessitates much less energy than a GPS device, meerkats would not have to be disturbed to record this data. Another advantage of the technique would be that several human observers are available to record many behavioural traits. The data so far did not enable to detect any "graded leadership" (Nagy et al., 2010; Šárová et al., 2010). However, such leadership might still be present, particularly if older individuals have better knowledge of their territory. The available GPS data also allowed us to calculate the average speed of our focal meerkats. This speed was ~ 6.3 $m.min^{-1}$, which is about twice as much as the average speed of a meerkat group (~ 3.2 m.min-1, Bousquet et al., 2011). It indicates that the individuals' trajectories of meerkats are much more winding than their group's trajectory.

The potential of the available techniques of location recordings and social network analysis are highly promising but are only efficient when many data points are readily available. The facts that these techniques can be adapted to meerkats and that our data already suggest that the observed variation is higher than the one expected by chance should encourage further investigation of the role of spatial positioning in meerkat groups.

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CHAPTER 5

Resolution of Experimentally Induced Symmetrical Conflicts of Interest in Meerkats (*Suricata suricatta*)

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Resolution of Experimentally Induced Symmetrical Conflicts of Interest in Meerkats (*Suricata suricatta*)

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Summary

Activity shifts in animal groups are a potential source of group fragmentation if members do not coordinate themselves. This coordination can become further complicated when individuals within a group face conflicts of interest. Here, we experimentally induced symmetrical conflicts of interest over which direction to choose in meerkat groups. We trained dominant and subordinate individuals to expect food at locations in opposite directions when the group was still at its sleeping burrow (i.e., before the group started foraging). Trained individuals were more likely to initiate group departure in the direction of their rewarded location and there was no difference between dominants and subordinates in initiation rate. Initiation of group departure seemed to be the most important factor determining the final direction of the group, as the direction chosen by the first initiator was rarely challenged afterwards. We did not observe any obvious signals used to enhance recruitment during this process. Over the experimental days, initiator identity changed suggesting that individual motivation to initiate group departure varies from day to day. All together, meerkats voluntarily avoided immediate foraging benefits to maintain cohesion with the group, which likely prevents them from incurring costs associated with becoming isolated. We conclude that individuals refrain from initiating group splits when conflicts of interest are low and any individual can take the lead, often without the use of obvious signals other than the displacement itself.

Keywords: symmetrical conflict of interest; meerkat; cohesion benefit; isolation cost; variable movement initiation

1. INTRODUCTION

Many animal groups remain spatially cohesive even when their group members shift activity or direction of travel. In order to achieve cohesion, individuals within a group have to coordinate themselves. The coordination phase can be seen as a phase during which mechanisms enable group members to aggregate their individual behaviours into group-specific behaviour. These aggregation rules "assign to each combination of individual inputs a resulting collective output" (Conradt & List, 2009) and therefore link the individual-decision level to the group-decision level. This can be done by using self-organisation rules (Camazine et al., 2001; Couzin et al., 2005; Sumpter, 2006) or through specifically evolved signals (Black, 1988; Stewart & Harcourt, 1994; Boinski & Campbell, 1995; Prins, 1996; Bousquet et al., 2011).

The success of the coordination phase also depends on the presence of conflicts of interest within the group, either due to differences in individual requirements or to the different information sets group members possess (Biro et al., 2006; King et al., 2008). Substantial conflicts of interest can even lead to complete social segregation. For instance, in sexually dimorphic ungulates, temporal activity budgets differ widely between sexes and cause complete sexual segregation in some of these species (Ruckstuhl & Neuhaus, 2002). However, in many species, groups remain cohesive even when strong conflicts of interest occur (King et al., 2008). The study of conflicts of interest can help to elucidate the characteristics of individuals able to dictate their own interest to others (King et al., 2008) but also to understand how a group can remain united despite these conflicts (Prins, 1996).

Research on conflicts of interest has received a lot of theoretical modelling (temporal conflicts: Conradt & Roper, 2003; Rands et al., 2003; Dostálková & Špinka, 2007; Rands et al., 2008; directional conflicts: Couzin et al., 2005; Conradt & Roper, 2009; Conradt et al., 2009) and observational attention (Kummer, 1968; Rees, 1987; Prins, 1996; Boinski, 2000; Conradt & Roper, 2005; King et al., 2009). However, empirical tests of the effects of conflicts of interest are still rare (Sumpter & Beekman, 2003; King et al., 2008; Dyer et al., 2009; Harcourt et al., 2010), potentially because it can be difficult or unethical to elicit conflicts of interest within animal groups. Symmetrical conflict experiments, in which the reward for informed individuals is identical, have only been conducted in ants (Sumpter & Beekman, 2003), fish (Harcourt et al., 2010) and humans (Dyer et al., 2009). The only

nonhuman mammal work that has been done was an asymmetric study in chacma baboons (*Papio ursinus*) where researchers induced asymmetrical conflicts by presenting foraging groups one extra foraging patch (which only the dominant male was able to monopolise) without any symmetrical incentive in another direction for subordinate individuals (King et al., 2008). Therefore, dominance and information are confounded. Consequently, an experiment on symmetrical conflicts of interest in stable social groups of mammals will help to strengthen our understanding of conflict resolution by controlling for the effect of asymmetry, enabling to identify the influence of the different factors.

Meerkats are small carnivores living in stable social groups with high reproductive skew in favour of the dominant individuals, indicating strong reproductive conflicts of interest (Clutton-Brock et al., 1999b). Meerkat groups typically consist of individuals of both sexes and any age category (Doolan & Macdonald, 1997). Besides birth, death and rare events of inter-group migrations by males or fissions, meerkat group composition remains stable for years. Therefore, there is a high potential for variation between individuals' energetic requirements or territorial knowledge, which can lead to potential conflicts (Boinski, 2000). However, little is known about motivational (*i.e.*, what to do?) and/or directional (*i.e.*, where to go?) conflicts of interest in mongooses.

Meerkat groups forage cohesively, whereby they do not share food among each other (Doolan & Macdonald, 1996). They typically travel 500 m to 2 km per day mainly in their territory, which they defend fiercely against neighbouring groups (Jordan et al., 2007). They are highly vocal and coordinate their spatial movement with several different types of calls (Manser, 1998). They use "lead" calls in the morning to coordinate their group departure from the sleeping burrow (Manser, 1998; Turbé, 2006). During foraging they constantly emit "close" calls, which seem to function to maintain cohesion (Manser, 1998; Townsend et al., 2010), and in addition they give "moving" calls to initiate movement from one foraging area to another (Bousquet et al., 2011). Recent work suggests that physiological incentives appear to elicit meerkats to lead the group away from the morning sleeping burrow (Bousquet et al., in prep.). However, we still do not know how meerkat groups remain cohesive despite conflicting information about the environment among group members. To assess this situation, one way is to give artificial and controlled additional information

to specific individuals in the group to induce conflicts of interest over which direction to take.

We experimentally induced directional conflicts of interest between two focal individuals, a dominant and a subordinate, before their group departed for foraging from the morning sleeping burrow. The induced conflicts were symmetrical by keeping the reward equivalent for each individual. We specifically investigated: i) whether dominant individuals were more likely to attract the group in their direction of interest; ii) whether meerkats changed direction and/or initiator within a morning departure by comparing the identity and the direction of the first initiator to the identity and the direction of the final initiator; iii) whether the same individual wins the conflict of interest repeatedly by conducting the experiment on 5 consecutive days. Furthermore, we determined whether our focal individuals actively tried to attract their group members by the use of lead calls.

2. MATERIALS AND METHODS

(a) *Study site and population*

We studied conflicts of interest on a wild but habituated population of meerkats at the Kalahari Meerkat Project, South Africa. The project is located on ranchland in the Kalahari, near Van Zylsrus (26° 58' S, 21° 49' E). Description of habitat and climate are provided elsewhere (Clutton-Brock et al., 1999a; Russell et al., 2002). All animals in the population could be individually identified by the use of unique dye mark combinations. Individuals were habituated to close observation (< 1 m). The ages of over 95 % of individuals were known precisely (± 5 days) as well as most of their life-history events.

(b) *Training phase*

We conducted this experiment on 5 different meerkat groups from July to October 2008, ranging in group size from 9 to 17 individuals (mean ± s. e.: 13.4 ± 1.6). In each group, we trained the dominant female and the next-in-line subordinate female (of similar age as the dominant female) to feed from two different specific shapes (one for each individual) baited with frozen scorpions (one of meerkats' favourite prey, Doolan & Macdonald, 1996). However, as in one group (Frisky) the next-in-line subordinate females were all evicted during the period of the

experiments, we trained the group's dominant male and the next-in-line subordinate male. Results from this group do not suggest any sex difference in behaviour. During non-breeding periods dominants and subordinates do not differ in their ability to lead the group in the morning (Bousquet et al., in prep). However, when lactating females are present in a group, they very often lead the group departure (Bousquet et al., in prep.). In our study, none of the females were lactating, therefore ensuring an identical leading probability for the two trained individuals. Furthermore, dominant and subordinate individuals do not differ in their ability to be followed during foraging trips (Bousquet et al., 2011).

To attract the target individuals to the food locations, we used 6 obviously different types of shapes (a green circle, a white triangle, a yellow star, a black rectangle, a purple moon and a yellow-and-black Y, all with an area of 210 cm^2); as used by Thornton & Malapert (2009b, see their Table 1). In the specific groups, we always used different group-shape combinations from their study, and more than two months had elapsed between the two studies, reducing the possibility of habituation to the shapes. The scorpions used as rewards were collected at the study site and brought back to the farmhouse where they were frozen until used for the experiment. For all presentations, we placed a frozen scorpion below the shape. The shape was mounted on a tray which was covered by sand. To make the shape more conspicuous to the meerkats, we put the tray on a box (20 cm high) and exposed the scorpion's tail outside of the sand. Meerkats therefore had to dig in order to access the scorpion, mimicking a natural situation.

The training phase lasted 6 days. Each morning, we arrived at the sleeping burrow before any meerkat had emerged. Once all group members were out from their burrow, one observer presented the specific shape with scorpion reward on its tray to the focal animal. When meerkats other than the focal individual were approaching the shape, we gently removed the shape until the meerkats moved away. We then started again to approach the focal individual. On the first days, we presented the shapes close to the sleeping burrow entrances (within 1 m). Then, we moved the shape further away from the burrow, up to a maximum of 10 meters. All individuals were already well habituated to the process after 5 days but we continued for 1 more day to improve the habituation even more. During the training phase, each focal individual received 3 scorpions on the first morning and 2 scorpions for each successive training

morning, totalling 13 scorpions per individual for the whole period. We left a one-day break between the end of the training phase and the beginning of the test phase.

(c) *Test phase*

We firstly placed the two shapes used during the training phase in diametrically opposed directions. As observed in a previous study (Christophe Bousquet, unpublished data) we know that meerkats have a preferential leaving direction (towards East, the direction of the sun). Therefore, we avoided the orientation East – West as often as we could or made sure to have the symmetrical arrangement on another test day (so that each shape was facing East on the same number of test days). Overall, the East – West orientation was used in only 4 trials out of 24. The distance between the shape and the sleeping burrow during the test days was assessed by GPS (GPS GARMIN eTreX H, accuracy: 95 % of fixes within 5 meters) and was consistently around 20 m (20.42 ± 0.91 m), which was further than during the training phase. We increased the distance between shapes on test days to ensure a stronger conflict between trained individuals. Yet, each shape was still visible from the sleeping burrow. On test days, each shape was baited with a frozen scorpion and all individuals had potential access to the shapes. Thus, unlike during the training phase, we did not remove the shape when untrained meerkats approached it. Each meerkat group was tested for 5 consecutive days, except for one group (Lazuli), where we were only able to perform 4 tests because of the subordinate female eviction on the fifth day. Hence, we had a total of 24 tests from 5 different groups.

Once the first meerkat emerged, one observer videotaped the movements of the two focals and the same or another observer recorded movements of other individuals. We focused our attention on movements in the direction of either shape. For each morning, we therefore recorded the identity of the first individual in the group to move in a specific direction (the "first initiator"). For each focal individual, the chosen direction was classified in 3 categories: i) the "rewarded" direction if the focal individual went towards its rewarded shape; ii) the "non-rewarded" direction if the focal individual went in the direction of the other shape; and iii) the "other" direction in any other cases (Figure 1). When meerkats emerge from their burrow, they stand on their hind legs with their torso facing the sun to warm up. It was therefore easy to record an individual movement every time a meerkat left its sunning position and started walking in any direction for more than 1 m. However, this kind of

movement does not immediately make the group leave the burrow. Therefore, we also recorded the identity of the first individual to initiate the final group movement when the group leaves the burrow (the "final initiator") and its direction. The final direction was considered similar to the initial direction when it did not differ more than 45° from it. It is possible that our experimental design could have induced meerkat groups to split, at which point we would have stopped the experiment. However, during the whole experimental period, this never occurred. The study was carried out under licences issued by the Northern Cape Conservation Service and ethical committee of Pretoria University, South Africa.

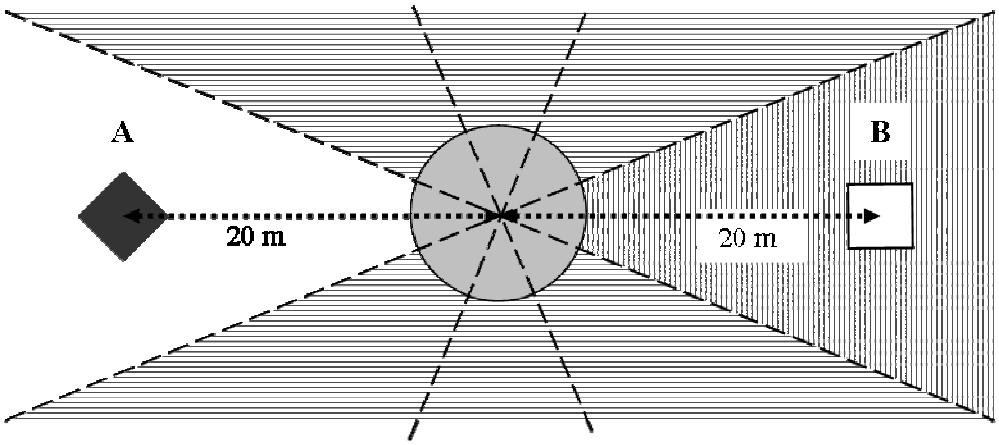

Figure 1. Overview of the experimental setting and of the corresponding zones. The light grey circle represents meerkats' sleeping burrow. Individual A was trained to receive food at the dark grey diamond (shape A), while individual B was trained to receive food at the white square (shape B). A movement of individual A in the white area of the figure was considered as a movement towards its rewarded shape A. A movement of individual A in the vertically stripped area of the figure was considered as a movement towards its non-rewarded shape B. Movements of individual A in the horizontally stripped area of the figure were considered as movements in other directions.

(d) ***Statistics***

All statistics were done with R 2.10.0 (R development core team, 2009). We used the binomial test with Yates' continuity correction to compare observed and expected proportions (Crawley, 2007). Expected values assume that the probability of each adult in the group is identical and are equal to the average of the reciprocal of the

number of adults for each test day in each of the five groups (Table S1). We used generalised mixed-effect models when our response variable was binary and when we wanted to control for group identity and/or for individual identity. The models used a quasibinomial error distribution and individual identity nested in group identity or only group identity as a random term. We compared models with only one fixed effect and individual nested in group as a random term to the null model with only the intercept as a fixed effect and the same random term. We used likelihood ratio tests to test whether the fixed factor explained a significant amount of the variance compared to the reduced model without the fixed factor. Since likelihood ratio tests against a Chi-square distribution tend to overestimate effect size (Faraway, 2006; Jaeggi et al., 2010), we used parametric bootstrapping with 1,000 Monte Carlo simulations to generate a distribution of likelihood ratios (LR) from the fitted parameter estimates and tested the observed LR against this distribution (Faraway, 2006; Jaeggi et al., 2010). All generalised mixed-effect models used the library lme4 (Bates & Maechler, 2009).

3. RESULTS

(a) *Efficiency of the training phase*

Trained individuals initiated group departure in 17 (73.9 %) out of the 24 test days, which was significantly more than expected by chance (chance value: 5, binomial test with Yates' continuity correction, $\chi^2 = 15.02$, d. f. = 1, $p < 0.001$, Figure 2A). Out of these 17 trials, trained individuals went 11 (64.7 %) times in the direction of their rewarded shape, 2 (11.8 %) times in the direction of the non-rewarded shape and 4 (23.5 %) times in another direction than any shape (generalised mixed-effect model, $Z = -2.43$, $p < 0.05$, Figure 2B). Over the whole test period, only 3 (30 %) out of 10 trained individuals ate a scorpion at their non-rewarded shape. Out of the 28 untrained adults (all the naïve adults in the five studied groups), only 1 (3.6 %) ate a scorpion at a shape.

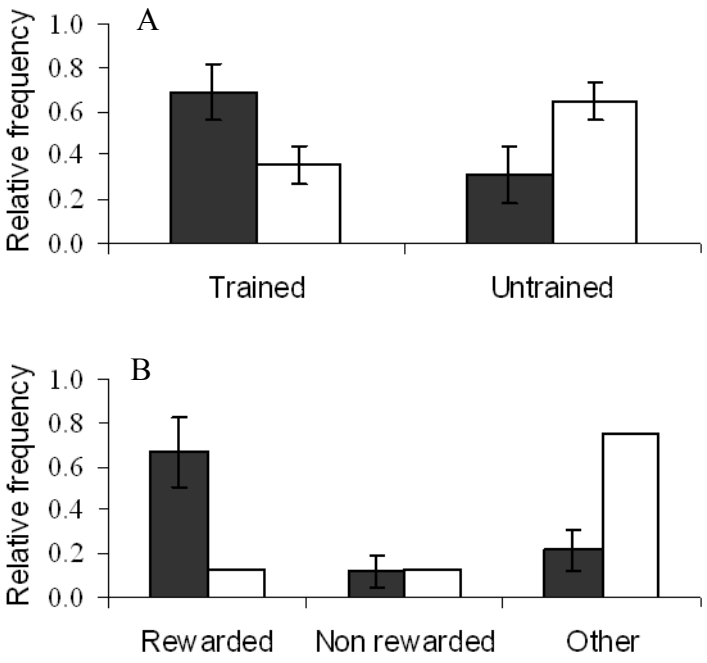

Figure 2. Relative frequency that: A) a trained or untrained individual initiated a group movement on test days; and B) a trained individual went in the direction of its rewarded shape ("Rewarded"), to the other one ("Non rewarded"), or in another direction ("Other"). Grey bars: observed relative frequency, white bars: expected relative frequency. Mean ± se, N = 5 groups.

(b) ***Effect of dominance status on the "first initiator" and the "final initiator"***

We detected no influence of dominance status on the ability of an individual to initiate the first movement to its specific shape. The subordinate trained individual initiated the first group movement in 10 (41.7 %) out of the 24 trials, and the dominant trained individual in 7 (29.2 %) out of the 24 trials (Monte-Carlo Likelihood ratio test between generalised mixed-effect models, LR = 1.06, d. f. = 1, $p = 0.34$, Figure 3A). The remaining 7 trials were days in which neither of the trained individuals initiated group movement. On these days, the first initiator was a subordinate male in 4 trials, the dominant male in 2 trials and another subordinate female in 1 trial.

As with the first initiator, we detected no effect of dominance status on the identity of the final initiator. The subordinate trained individual initiated the final group movement in 10 (41.7 %) out of the 24 trials, and the dominant trained

individual in 7 (29.2 %) out of the 24 trials (Monte-Carlo Likelihood ratio test between generalised mixed-effect models, LR = 1.17, d. f. = 1, $p = 0.25$, Figure 3B). The remaining 7 trials were days in which neither of the trained individuals initiated group movement, and the final initiator was a subordinate male in 5 trials, the dominant male in 1 trial and another subordinate female in 1 trial.

Dominant and subordinate individuals were as likely to initiate group movement in the early or late test period: session number did not have an influence on the dominance status of the first initiator (generalised mixed-effect model, $Z = 1.44$, $p = 0.15$) or of the final initiator (generalised mixed-effect model, $Z = 0.04$, $p = 0.97$). The time series of the initiators' identity are given in details in Table S2.

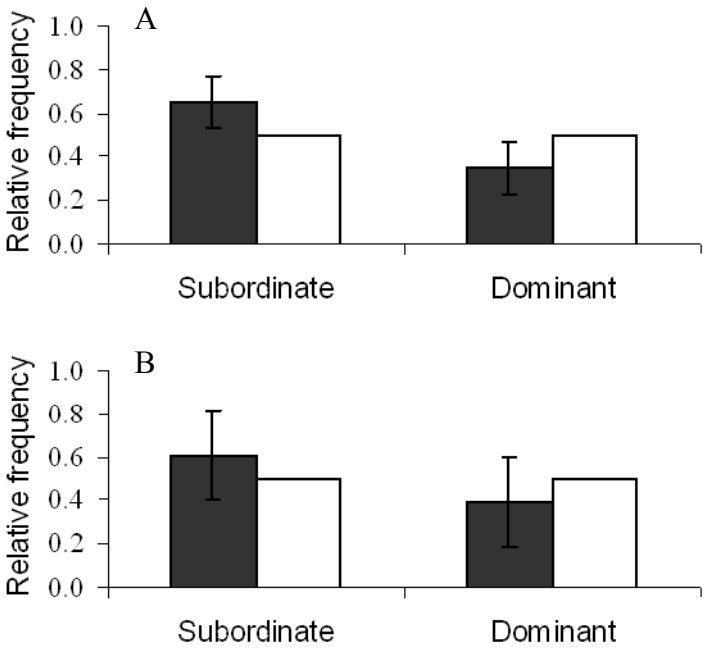

Figure 3. Relative frequency that the subordinate or the dominant trained individual initiated: A) the first group movement on test days; B) the final group movement on test days. Grey bars: observed relative frequency, white bars: expected relative frequency. Mean ± se, N = 5 groups.

(c) ***Consistency of initiator and direction***

The initial and the final initiators were the same individual in 17 (73.9 %) out of 24 trials. This consistency in individual identity is highly significant (binomial test with Yates' continuity correction, $\chi^2 = 53.83$, d. f. = 1, $p < 0.001$, Figure 4A). However, the consistency of the identity of the initiator was not higher when trained individuals initiated the first movement than when untrained individuals initiated it (70.6 % and 71.4 % respectively, generalised mixed-effect model, $Z = 0.04$, $p = 0.97$).

The overall observed difference between the "first direction" and the "final direction" was 49.3 ± 13.3°. The "first initiator" and the "final initiator" moved in the same direction (when their directions were differing less than 45°) in 16 (66.7 %) out of the 24 trials. In these trials, the observed difference between the two bearings was much less (7.06 ± 2.89°). This consistency of direction is much higher than the one expected by chance, if each 45° segment was as likely for the final initiator ($\chi^2 = 22.22$, d. f. = 1, $p < 0.001$, Figure 4B). From the 17 trials in which trained individuals initiated the first group movement, the final group movement was in the same direction as the first group movement in 11 trials (64.7 %). From the 7 trials in which other untrained individuals initiated the first group movement, the final group movement was in the same direction as the first group movement in 5 trials (71.4 %). Therefore, the consistency of direction was not higher when trained individuals initiated the first movement than when untrained individuals initiated it (generalised mixed-effect model, $Z = 0.32$, $p = 0.75$).

(d) ***Use of vocalisations***

During the test or the training phase, focal individuals never emitted lead calls or any other vocalisation while travelling in the direction of their shape. However, on 4 out of the 7 days when untrained individuals led the group, these untrained individuals emitted lead calls (Monte-Carlo Likelihood ratio test between generalised mixed-effect models, LR = 9.68, d. f. = 1, $p = 0.07$).

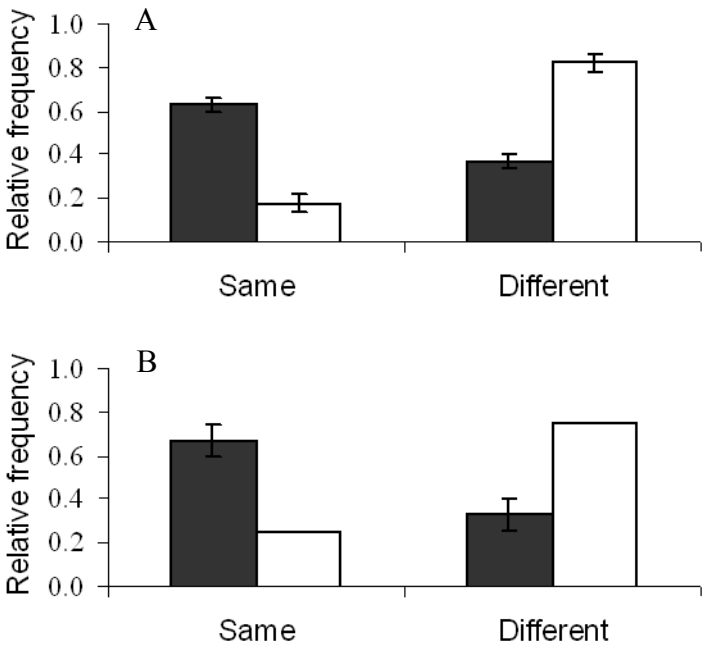

Figure 4. Relative frequency that: A) the final initiator was the same or different as the first initiator; and B) the final direction was the same or different as the first direction. Grey bars: observed relative frequency, white bars: expected relative frequency. Mean ± se, N = 5 groups.

4. DISCUSSION

The experimentally induced symmetrical conflicts of interest in meerkat groups showed that trained individuals initiated group departure to a specific food location more often than untrained individuals. We did not find any effect of dominance status on the identity of the "first initiator" neither on the identity of the "final initiator". However, the identity and the direction of the final initiator were consistent with the identity and the direction of the first initiator. Moreover, we did not detect any carry-over effect on the 5 days of test: early conflict outcomes did not influence the later ones. Trained individuals never emitted vocalisations when moving towards their rewarded shapes, whereas untrained individuals initiating group movement vocalised in more than half of their attempts.

Trained individuals were successful in attracting the group away from the sleeping burrow in the direction of their shape, to eat their reward. Thus, the immediate incentive of eating a scorpion was enough for trained individuals to initiate group departure. However, when a trained individual moved in the direction of its

shape, the other trained individual did not try to get access to its own rewarded shape, and followed the other group members, sometimes being among the first to join. Furthermore, group movement initiations by untrained individuals occurred on 7 days. On these days, none of the shapes was visited and we did not notice any effort of the trained individuals to reach their specific shape. We also did not find any significant effect of dominance on attraction success. Therefore, being the first to initiate the group movement seemed to be the most important for other group members to join. This result is in line with the findings of Turbé (2006) and an additional study of ours (Bousquet et al., in prep.) on the same population, which found leadership was influenced by the individuals' inner state (previous day's foraging success and female reproductive state). Thus, when an untrained individual led, it might have been because it was in a needier condition than trained individuals. Unfortunately, we could not rule out this hypothesis, as measuring relative need through weight data would have interfered with the departure process. However, our previous study showed that leading individuals had no higher morning foraging success (Bousquet et al., in prep.). Therefore, leading away from the burrow in meerkats may affect only immediate food intake and not over longer foraging periods. In all trials, trained individuals who did not leave first followed without trying to eat their reward, located in a different direction. It thus seems a priority for meerkats to follow an early initiator rather than to reach an individual reward. This can be due to the fact that meerkats' survival drastically decreases when on their own or in small groups (Clutton-Brock et al., 1999a). This propensity to follow any individual, independently of an individual's immediate interest, can also explain the observed consistency of direction and identity of the final initiator with respect to the direction and identity of the first initiator. Possibly because of this consistency, overt directional conflicts are rarely observed in meerkats and occur mainly in specific cases (2 cases in 18 months in the context of road crossing and 5 cases in 4 years when rovers tried to lead the group, Manser & Bousquet, pers. obs.).

However, this consistency of initiators and the scarcity of directional conflict within one morning do not mean that initiators are consistent between mornings. Indeed, over the 5 test days, both trained individuals in every group were followed by group members at least once in the direction of their shape. Therefore, the individual motivation to initiate group departure seems to vary from day to day. This fits in well with the concept of turn-taking in which individuals with conflicting information

alternate their leadership and therefore diminish the overall conflict costs (Harcourt et al., 2010). However, whether meerkats use this type of rule or whether it is a corollary of the effect of inner state on leadership still needs further research.

It is intriguing that trained meerkats did not emit lead calls while heading towards their rewarded shapes, as lead calls in meerkats are often used by an individual when initiating a group departure from the sleeping burrow (Turbé, 2006). Indeed, untrained individuals emitted lead calls on 4 out of the 7 days during which they were observed initiating group movement. By refraining from emitting lead calls, it is possible that trained individuals secure their sole access to an extra-food source, and did not try to initiate group movement to be followed at this stage. Specific signals can be important for recruitment in many species (Radford, 2004; Sueur & Petit, 2010). However, recruitment signals can also only be produced in specific contexts: subordinate green woodhoopoes for example do not emit vocalisations when they go away from the group to secure food access (Radford, 2004). As meerkats learn socially and individually when food is associated to a shape (Thornton & Malapert, 2009a,b), it might be advantageous to approach a shape as inconspicuously as possible. On the other hand, the trade-off between securing a food source and the motivation to reach the shape might not have been strong enough for trained meerkats to use vocalisations. It would be interesting to create a bigger conflict within each individual by putting the shapes even further away from the burrow (and potentially also by increasing the amount of extra-food to be expected). Then, trained individuals might have to use vocalisations to attract the group in order for trained individuals to access their reward without being isolated from the group.

From our results, we have shown that access to extra-food in meerkats elicited leading behaviour. However, this response was not as drastic as in a species in which some individuals can have a much higher resource holding potential (i.e., the ability to monopolise foraging resources, RHP) than others (King et al., 2008). Yet, the effect of RHP in King et al.'s study (2008) might have been so strong because the conflict was asymmetrical. In this case, group members with low RHP could not gain access to another food-enriched patch. In species with high RHP, symmetrical conflicts might either increase the probability of group fusion or reveal the appearance of turn-taking in the group decision-making process. In meerkats, RHP is more evenly distributed among individuals and we showed that no single trained individual

monopolised the choice of the group's direction consistently over the experimental days in symmetrical conflicts.

We conclude that even in species with high reproductive skew, directional conflicts appear to be related to the condition of an individual relative to the other group members (Turbé, 2006; Bousquet et al., in prep). This may ultimately result in frequent changes in leadership including all adult members, which has previously been highlighted as the basis for turn-taking behaviour (Harcourt et al., 2010). Generally, this is conceivable from an evolutionary standpoint, as fighting over reproductive control is of much higher importance for an individual's fitness than fighting for directional control, particularly in an environment where food is evenly distributed. Furthermore, it is known that individuals with too high a commitment to their own target increase a group's fragmentation risk (Conradt et al., 2009). In a species, where group cohesion is crucial to survival, it is not surprising to find voluntary avoidance of known foraging benefits to remain in the group and avoid the costs of being isolated.

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Group	Day	Ad	ExpTrained	ExpTrGrp	ExpTrMean	ExpTrSE	ExpSameInd	ExpSIGrp	ExpSIMean	ExpSISE
Aztecs	1	5	0.4000				0.2000			
Aztecs	2	5	0.4000				0.2000			
Aztecs	3	5	0.4000				0.2000			
Aztecs	4	5	0.4000				0.2000			
Aztecs	5	5	0.4000	0.4000			0.2000	0.2000		
Commandos	1	9	0.2222				0.1111			
Commandos	2	12	0.1667				0.0833			
Commandos	3	11	0.1818				0.0909			
Commandos	4	11	0.1818				0.0909			
Commandos	5	11	0.1818	0.1869			0.0909	0.0934		
Elveera	1	10	0.2000				0.1000			
Elveera	2	11	0.1818				0.0909			
Elveera	3	11	0.1818				0.0909			
Elveera	4	11	0.1818				0.0909			
Elveera	5	11	0.1818	0.1855			0.0909	0.0927		
Frisky	1	3	0.6667				0.3333			
Frisky	2	3	0.6667				0.3333			
Frisky	3	3	0.6667				0.3333			
Frisky	4	3	0.6667				0.3333			
Frisky	5	3	0.6667	0.6667			0.3333	0.3333		
Lazuli	1	5	0.4000				0.2000			
Lazuli	2	6	0.3333				0.1667			
Lazuli	3	6	0.3333				0.1667			
Lazuli	4	7	0.2857	0.3381	0.3554	0.0884	0.1429	0.1690	0.1777	0.0442

Table S1. Calculation of the expected values used in the main text. “Group” is the name of the focal group. “Day” is the test day number. “Ad” is the number of adults present in the group during the specified session. “ExpTrained” is the expected frequency of trained individuals to initiate a group movement, with the assumption that each adult have the same initiation probability. Because two adults were trained, it is equal to two times the reciprocal of the number of adults (number of adults varied between different days). “ExpTrGr” is the average frequency of trained individuals for each focal group. “ExpTrMean” is the average frequency of trained individuals for the five groups. “ExpTrSE” is the standard error of the average frequency of trained individuals for the five groups. “ExpSameInd” is the expected frequency that an individual being a first initiator would also be a last initiator, with the assumption that each adult has the same probability to be a last initiator. “ExpSIGrp” is the average frequency that the last initiator would be the same as the first initiator for each focal group. “ExpSIMean” is the average frequency that the last initiator would be the same as the first initiator for the five groups. “ExpSISE” is the standard error of the average frequency that the last initiator would be the same as the first initiator for the five groups.

Group	Sess1	Sess2	Sess3	Sess4	Sess5
First initiator					
Aztecs	SUB	OTH	DOM	DOM	DOM
Commandos	DOM	SUB	SUB	DOM	SUB
Elveera	SUB	SUB	DOM	OTH	OTH
Frisky	SUB	SUB	DOM	SUB	OTH
Lazuli	OTH	SUB	OTH	OTH	
Last initiator					
Aztecs	OTH	SUB	DOM	DOM	DOM
Commandos	SUB	SUB	SUB	DOM	SUB
Elveera	SUB	SUB	OTH	OTH	OTH
Frisky	DOM	DOM	DOM	SUB	OTH
Lazuli	OTH	SUB	SUB	OTH	

Table S2. Time series of the results over the five days for the five groups. "DOM" means that the dominant trained individual initiated the group movement, "SUB" means that the subordinate trained individual initiated the group movement and "OTH" means that an untrained individual initiated the group movement. Grey boxes identify cases in which the last initiator differs from the first initiator.

GENERAL DISCUSSION

General Discussion

In the last 5 data chapters, I focused on the diversity of several aspects of group decision-making in meerkats. I showed that leadership in two temporally close different contexts depend on different variables: emergence order was mainly predicted by individual identity whereas leaving order negatively correlated with previous day foraging success. I then showed how group burrow renovation is reached by social facilitation as an aggregation rule. I also found that foraging meerkat groups use a quorum threshold of individuals emitting moving calls before increasing group speed and changing foraging patch. Additionally, I presented data on individual positions within the group: meerkats form small sub-groups of non-random composition during their foraging trips. Finally, I showed that small conflicts of interest are not enough to break down group cohesion: meerkats prefer following fellow group members rather than eating a reward located in another direction. In this concluding chapter, I will bring all these different aspects together. First, I emphasize the importance for meerkats of keeping the cohesion of the group. Second, I highlight the so far underestimated role of followers in group decision-making. Third, I stress the role of spatial positioning in animal groups. Lastly, I discuss the importance of integrating the individual behavioural consistencies of each group member in studies on group-decision-making.

1. THE IMPORTANCE OF GROUP COHESION FOR MEERKATS

Meerkats are medium-sized animals living in open habitat and, to meet their energetic needs, they prey on invertebrates buried in the ground. While doing so, they dig for important amounts of time without being able to look around for predators. Furthermore, contrary to Cape porcupines with their spines or to ground pangolins with their scales, they do not possess any specific defensive weapon. Therefore, on their own, meerkats can be easily detected and eaten by predators with good vision (Clutton-Brock et al., 1999a). An important adaptation to these constraints is to form groups in which vigilance is more distributed among individuals and therefore predators more easily spotted (Powell, 1974; Clutton-Brock et al., 1999c). Besides these predation-related issues, meerkats also face difficulties to rear young on their own. One way for meerkats to tackle these difficulties is to rear young cooperatively

(Clutton-Brock et al., 2001) and, as expected for cooperative breeders, female fecundity as well as pup survival increase with group size (Clutton-Brock et al., 1999a; Hodge et al., 2008). Therefore, meerkats do possess strong incentives to live in a group as large as possible. However, whether or not the results found in this PhD thesis also apply to large meerkat groups (over 30 group members) still needs further research and may lead to interesting comparisons.

Meerkat groups are of heterogeneous composition with individuals of both sexes and of various ages living together (van Staaden, 1994). In addition, dominant individuals monopolize the reproductive role in the group (Clutton-Brock et al., 1999b). As a result, it is likely that individuals differ much in their optimal needs, which could render the maintenance of group cohesion more difficult to achieve, particularly during activity shifts (Conradt & Roper, 2000). Indeed, individuals for whom the new activity is not optimal at that moment will have to abide by the group's decision to continue benefiting from other group advantages. This discrepancy between an individual's optimal behaviour and its group's actual behaviour is termed "consensus cost" for that individual (Conradt & Roper, 2005). Group cohesion can be rendered easier when individuals monitor the behaviour of their fellow group members (Sueur & Petit, 2010) or when they communicate via specific signals among each other (Dostálková & Špinka, 2007). Indeed, communication increases the information exchange about each other's actual or future needs or actions and therefore enables easier coordination. It thus allows a reduction in overall consensus costs. However, the need of communication with specific obvious signals is beneficial only under specific conditions: when "communicating is cheap" and when "acting later is cheaper than acting prematurely" (Dostálková & Špinka, 2007).

Meerkats maintain group cohesion through many different mechanisms, the variety of which proving by itself how group cohesion is important for them. First, as we have seen in Chapters 1 and 5, individuals leaving the sleeping burrow area to start foraging do not necessarily need to advertise their movement by specific signals (lead calls are not always produced in this context). Yet, these silent animals are still successful in attracting the rest of the group. Thus, at least some individuals do monitor visually the behaviour of these silent individuals and adjust to it by mimicking it (Sueur et al., 2009). This inclination of individuals to follow any leaving individual has obviously a positive impact on group cohesion (Pillot et al., 2010). Second, when necessary, meerkats can use signals to more actively ensure group

cohesion. For instance, during foraging, meerkats use moving calls before changing foraging patch. This signal is only fully efficient when a quorum of 2 to 3 individuals produce it at the same time (Chapter 3). If, while foraging, the probability to call increases when an individual estimates that the quality of the current foraging patch is getting poorer, then the use of this quorum threshold will increase the likelihood of a correct decision (i.e., when to move to a higher quality location) at the group level (Sumpter & Pratt, 2009). Furthermore, this signal matches the predictions of Dostálková & Špinka (2007): the signal is cheap (a few vocalizations) and remaining longer in a potentially deprived patch is cheaper than leaving a plentiful one. Finally, meerkats tend to avoid directional conflicts. The results from an experiment inducing conflicts among two group members over the direction in which to go to receive extra-food (through the use of specific shapes as targeted visual signals) showed that such a "conflict" was simply solved by the use of the individual rule: "follow the first individual to leave, even if it is not going in the direction of my reward" (Chapter 5). On the first day, one individual moved off in the direction of its shape and got the reward. Its "opponent" did not try to move in the direction of its own shape and followed the other individual. The reverse was true on other days of the experiment. Furthermore, this "conflict" was not systematically won by the dominant individual, which is different from the conflicts meerkats face in relation to reproduction (Clutton-Brock et al., 1999b). The peaceful resolution of the experimentally induced conflict can also explain why overt directional conflicts are rarely seen in meerkats.

2. THE ROLE OF FOLLOWERS IN GROUP DECISION-MAKING

Traditionally, animal group movements have been seen as resulting from an individual manipulating other group members to move. Such individuals were considered as leaders and were usually thought to be unique within the group (Schaller, 1963; Kummer, 1968). Later, research insisted on the fact that leaders are not consistent across contexts or over time (Reinhardt, 1983; Lamprecht, 1992). This variability in leadership had to be explained. Several factors have been found to influence who will become a leader in a specific context. First, as the early researchers expected, the identity of the individual itself can be an important predictor of being a leader (Fischhoff et al., 2007). However, this traditional view had to be broadened by including factors such as level of hunger (Fischhoff et al., 2007;

Conradt et al., 2009), resource holding potential (King et al., 2008), personal information (Lusseau & Conradt, 2009) and personality (Kurvers et al., 2009). In meerkats, hunger level and individual identity seem to be important predictors of leadership (Chapter 1). However, whether or not the importance of individual identity can be due to an effect of personality needs more work to be carried out. Theoretically, hunger levels are now considered to have a drastic effect on leadership (Rands et al., 2003; Rands et al., 2008; Conradt et al., 2009; Sumpter, 2009). Yet, whether or not this hunger level is related to direct foraging advantages is not routinely checked (but see Fischhoff et al., 2007 for a counter-example).

Because leadership is variable over time or contexts and often driven by hunger levels, which are not identical for each individual, a research question recently emerged: why do individuals engaged in other activities follow leaders (King, 2010)? First, particularly in the morning, meerkats are usually good at following each other: the final leaving direction is often the same as the first moving direction, indicating rare shifts of direction (Chapter 5). Therefore, followers are often reluctant to change the direction chosen by the first moving individual. Furthermore, at least for the first three individuals, the latency between individuals decreases in both leading processes investigated in Chapter 1. Indeed, for the emergence order and the leaving order, the latency between the third and the second individuals was significantly lower than the latency between the second and the first individuals (Chapter 1). However, followership is not always granted and when initiators fail to recruit other group members, they usually turn back to the rest of the group (Radford, 2004; King, 2010). In meerkats, if an individual emitting moving calls is not followed by other callers, it will also remain in the group and not accelerate (Chapter 3).

With this in mind, one can now envision leadership as a negotiation between initiators and followers. Therefore, it will become increasingly more important to report all sequences of group decision-making from the first intentions up to the final group decisions (Sueur et al., 2009, 2010, 2011). Such negotiations have been observed in several species. When released on their own, pigeons learned an individual route to come back to their home. This individual route is learnt and similar from trip to trip. However, different pigeons have different routes. When paired, if they have not too disparate routes, the two pigeons will travel home by using a new route, intermediate between the two original ones, which tend to testify that both pigeons negotiated. However, if the discrepancy between the two routes is too

substantial, one of the pigeon will become the leader and the other one will follow (Biro et al., 2006). It has been found that the individual emerging as the leader in this setting is the individual with the highest fidelity to its own route, even if this route is longer (Freeman et al., 2011). Therefore, the consensus among the two pigeons is as much due to the leader showing his route than to the follower who has been able to concede the use of its own route. This process also allows a majority of individuals to attract easily a minority of individuals, even when individuals cannot assess whether they are part of the minority or not (Couzin et al., 2005; Dyer et al., 2009).

Followers can also be attracted to an initiator's activity by social facilitation (Zajonc, 1965; Clayton, 1978). This is particularly the case in stationary groups, as evidenced by burrow renovation in meerkats (Chapter 2). Such aggregation rules of individual behaviours necessitate a high responsiveness of at least some individuals to the behaviours of other group members. Individuals with high responsiveness engage readily in such behaviours whereas individuals with low responsiveness never do. Indeed, some meerkats never renovated over the whole course of the study (Chapter 2). This leaves place to consistent individual behaviours which are documented to play a more and more important role in research on group decision-making (Kurvers et al., 2009; Kurvers et al., 2011; Michelena et al., 2010).

3. SPATIAL POSITIONING WITHIN ANIMAL GROUPS

We found that adults and dominants are more often in the front of the foraging meerkat group than other social categories (Chapter 4). Furthermore, foraging meerkats were forming well-differentiated sub-groups, with more individuals avoiding or preferring each other than expected by chance (Chapter 4). However, potentially due to the small sample size, it was not possible to determine whether specific individual classes were more central than others in the group network. This contrasts with studies in other species. For instance, in spider monkeys, females were found to be more central than males, even if associations among females were not different from random associations (Ramos-Fernández et al., 2009). It would be interesting to assess whether the differences in network centrality for various social categories also influence participation in group decision-making. In this case, female spider monkeys, which are central in their group network (Ramos-Fernández et al.,

2009) might also have more influence on group decisions than female meerkats, which are not central in their group network (Chapter 4).

Results from the GPS tracks recorded for each individual of the meerkat dominant pair showed that the dominant male and the dominant female did not differ in their travel length or in the amount of time each individual was in front of the other. This contrasts with results found in pigeons, in which the most dominant individual has the shortest track (Nagy et al., 2010). The results for meerkats might indicate that the dominant male and the dominant female have nearly the same level of influence on the group trajectory. However, to assess whether dominant individuals in meerkats have higher influence on group trajectory than subordinates, it is necessary to equip more individuals with GPS recording units from the same group than what was possible for this study. Individual variation over travelled distances is likely to occur in meerkats, as the average speed of the dominants was approximately twice as high as the average group speed. Therefore, in meerkats, the individual distance is much higher than the group distance, which allow researchers to tear apart more easily individuals from each other (Isbell et al., 1999).

4. INDIVIDUAL VARIATION AND GROUP DECISION-MAKING

Meerkats vary consistently from one another in their propensity to emerge first (Chapter 1) and to renovate the sleeping burrow (Chapter 2). If emerging first is linked to higher predation risk, some meerkats are consistently refusing to take the risk. In the same line, meerkats who never contribute to burrow renovation still have the advantages of a clean and fresh burrow, but without the cost of renovation itself. Because of the increasing evidence of the existence of a cooperative syndrome in meerkats (English et al., 2010; Madden & Clutton-Brock, 2011), it seems also unlikely that these low-contributors in renovation would be involved in other cooperative behaviours. Such individuals are often considered as “cheaters” or “freeloaders” (Trivers, 1971; Avilés, 2002).

Overall, group decisions can be seen as a form of cooperation, as some individuals are ready to give in their optimal activity to remain in the group and therefore face costs (Conradt & Roper, 2005; Chapter 5). Meerkats in a group are most often relatives, despite the occasional presence of unrelated individuals (Doolan & Macdonald, 1997). Therefore, meerkats are more likely to cooperate in group

decisions to increase their inclusive fitness (Hamilton, 1964a,b; Nowak et al., 2010) than to cooperate and expect a form of reciprocity from other group members later on (Trivers, 1971; Clutton-Brock, 2009). However, it is still difficult to understand why some individuals contribute more than others in certain group activities, and particularly why "cheaters" contribute as little and are still accepted in the group (Avilés, 2002).

Recent studies may have found a potential solution: groups with a mix of "cheaters" and "co-operators" do better than groups of only "cheaters" or only "co-operators" (MacLean et al., 2010; Pruitt & Riechert, 2011). Therefore, it seems that even "co-operators" benefit from the presence of "cheaters" in their group. This counter-intuitive result warrants seeking for likely explanations. First, the number of cheaters within a group auto regulates, because when the proportion of cheaters within a group increases, the incentive to remain in a group decreases (Avilés, 2002). Furthermore, uncooperative members can either be badly rated (Johnstone, 2001; Earley, 2010) or punished by other cooperative group members (Clutton-Brock & Garber, 1995). So, in the case of meerkats, if they are too many low contributors to burrow renovation, then the burrow quality will deteriorate faster and either the group has to change burrow more frequently or some individuals need to increase their contribution to the group task. Second, "cheaters" might only be considered cheaters as long as researchers do not understand their relevant role within the group. For instance, spiders from a social species, the comb-footed spider, were considered displaying either the "asocial" or the "social" phenotypes (Pruitt et al., 2008) until further research reclassified them as "aggressive" and "docile" phenotypes, respectively (Pruitt & Riechert, 2011). In meerkats, having uncooperative individuals within the group might maximise the inclusive fitness of other meerkat group members. This counter-intuitive hypothesis stands from the fact that prospecting at other group for reproductive opportunities is costly (Young et al., 2005) and that uncooperative meerkats do gain more weight than cooperative ones (Russell et al., 2003). Therefore, allowing some meerkats to bypass cooperative behaviours could be exchanged against indirect fitness benefits when an uncooperative meerkat leave its natal group and successfully establish itself as dominant in another group (Doolan & Macdonald, 1996). When dominant in its new group, the former uncooperative individual would monopolise reproduction (Griffin et al., 2003) and therefore increase the inclusive fitness of the group members of its natal group. Thus, individuals

considered as being uncooperative in one context might still be cooperative in other contexts. In this way, research on group decision-making need to integrate the effect of long-term consequences of the level of participation to group activities, which can be seen as a form of division of labour (Clutton-Brock et al., 2004; Arnold et al., 2005). Third, cooperative activities often depend upon energetic levels of the group members (Clutton-Brock et al., 2001; Barta et al., 2011). In this case, "cheaters" do not contribute as much as others when their energetic reserves are low. Once they increased their condition, "cheaters" can become cooperative, as is the case for helping behaviour in meerkats (Russell et al., 2003).

5. CONCLUSIONS AND FUTURE RESEARCH

Meerkats use a wide range of group decision-making mechanisms, including consensus decisions. Furthermore, meerkats use specific signals within the group, but not always. However, even when individuals do not use signals, the group remains cohesive due to the high responsiveness of individuals towards each other. This responsiveness favours the cohesion of the group and prevents meerkats from venturing out of the group, even when they have incentives to do so.

When it is ecologically important for individuals to remain in a cohesive group, it has to be expected that some individuals will give up their optimal activity to follow other individuals. Thus, what determines an individual to follow others is as important to understand as what determines an individual to lead. Indeed, an initiator who does not monitor the behaviour of its potential followers is less likely to succeed in becoming a leader. Furthermore, within a group, individuals do show consistent differences among each other, either resulting from a form of division of labour and/or from various personality traits. Therefore, integrating concepts from the literature on division of labour and personality should be rewarding for any further study on cooperation or group decision-making. Finally, taking advantage of recent techniques able to record precise individual location of individuals should increase our understanding of how spatial structure influences group decisions.

Because of all these factors, meerkats are an exceptional study species for researchers working on group decision-making. Meerkats have to remain in cohesive groups to increase their fitness. They are also easy to work with to carry out accurate observational protocols and to conduct experimental setups. Future research should

focus on group activity transitions, which are more and more often considered as a continuum. To understand precisely this continuum, one could look at the whole sequence of an activity change, from the first individual to the last individual involved. One should also look closely at the behaviour of "non-cooperative" individuals and assess their role in the group or group decision processes. Additionally, one could deepen the analysis of the influence of individual positions and trajectories on the group's foraging route and on the rate of interactions among individuals. Finally, one could determine up to which limit a single meerkat weighs more its membership to the group than an isolated reward.

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Appendix – Biological classification of the species presented in the text

Kingdom
- Class
  - Family
    - Species

Amoeboid (Amoebozoa)
- Social amoebae (Dictyostelia)
  - Dictyosteliidae
    - Slime mould — *Dictyostelium discoideum*

Plants (Plantae)
- Monocotyledons (Liliopsida)
  - Grass family (Poacea)
    - Lovegrass — *Eragrostis* spp.
    - Threeawns — *Aristida* spp., *Stripagrostis* spp.
    - Sourgrass — *Digitaria insularis*
    - *Schmidtia* spp.
- Dicotyledons (Magnoliopsida)
  - Trumpet-creeper family (Bignoniaceae)
    - Three-thorn — *Rhigozum trichotomum*
  - Pea family (Fabaceae)
    - Camel-thorn — *Acacia erioloba*
  - Caper family (Capparaceae)
    - Shepherd's tree — *Boscia albitrunca*

Animals (Animalia)
- Insects (Insecta)
  - Bees (Apidae)
    - Western honey bee — *Apis mellifera*
  - Ants (Formicidae)
    - New world army ant — *Eciton burchellii*
- Ray-finned fishes (Actinopterygii)
  - Minnows (Cyprinidae)

Golden shiner	*Notemigonus crysoleucas*
Sticklebacks (Gasterosteidae)	
Three-spined stickleback	*Gasterosteus aculeatus*
Reptiles (Reptilia)	
Cobras (Elapidae)	
Cape Cobra	*Naja nivea*
Vipers (Viperidae)	
Puff adder	*Bitis arietans*
Birds (Aves)	
Drongos (Dicruridae)	
Fork-tailed drongo	*Dicrurus adsimilis*
Hornbills (Bucerotidae)	
Southern yellow-billed hornbill	*Tockus leucomelas*
Plovers (Charadriidae)	
Crowned lapwing	*Vanellus coronatus*
Pigeons (Columbidae)	
Common pigeon	*Columba livia*
Geese (Anatidae)	
Barnacle goose	*Branta leucopsis*
Ostriches (Struthionidae)	
Ostrich	*Struthio camelus*
Eagles (Accipitridae)	
Martial eagle	*Polemaetus bellicosus*
Pale chanting goshawk	*Melierax canorus*
Mammals (Mammalia)	
Bovids (Bovidae)	
Hartebeest	*Alcelaphus buselaphus*
Springbok	*Antidorcas marsupialis*
Cattle	*Bos taurus*
Blue wildebeest	*Connochaetes taurinus*
Gemsbok	*Oryx gazella*
African buffalo	*Syncerus caffer*
Eland	*Taurotragus oryx*

Canids (Canidae)	
Black-backed jackal	*Canis mesomelas*
Old-world monkeys (Cercopithecidae)	
Chacma baboon	*Papio ursinus*
Dolphins (Delphinidae)	
Bottlenose dolphins	*Tursiops truncatus*
Felines (Felidae)	
Caracal	*Caracal caracal*
Herpestids (Herpestidae)	
Yellow mongoose	*Cynictis penicillata*
Slender mongoose	*Galerella sanguinea*
Banded mongoose	*Mungos mungo*
Meerkat	*Suricata suricatta*
Hominids (Hominidae)	
Human	*Homo sapiens*
Hyaenas (Hyaenidae)	
Aardwolf	*Proteles cristata*
Old-World Porcupines (Hystricidae)	
Porcupine	*Hystrix africaeaustralis*
Hares (Leporidae)	
Cape hare	*Lepus capensis*
Pangolins (Manidae)	
Ground pangolin	*Manis temminckii*
Aardvarks (Orycteropodidae)	
Aardvark	*Orycteropus afer*
Pedetidae	
Springhare	*Pedetes capensis*
Squirrels (Sciuridae)	
Ground squirrels	*Xerus inauris*

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